

Structural niche, limb morphology and locomotion in lacertid lizards (Squamata, Lacertidae); a preliminary survey

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SYNOPSIS. Lacertid lizards occur in a wide range of structural habitats and 1) may be found on open ground ranging from rocky surfaces, gravel and soil to firm and loose sand, or 2) be associated with quite dense low ground vegetation, or 3) climb through and over vegetation matrixes such as tall grass and herbs, bushes and tree canopy, or 4) climb on more or less continuous steep or even overhanging surfaces such as rock faces and tree boles. Some forms are largely confined to one of these broad structural niches while others occur more widely, but the locomotory requirements of the habitat occupied are usually reflected in morphology. The body may show some elongation in taxa that regularly travel through complex interstices of vegetation and similar habitats while it is quite short in forms that live on open ground; the tail is often extremely long in matrix climbers and may help spread weight in these.

When forelimb span/hindlimb span is plotted against hindlimb span/ head + body length, lacertids group substantially according to their structural niche. In general, disparity in span of the limb pairs increases with hindlimb length: long hind and short fore limbs occur in open ground forms, shorter more equal limb pairs in climbers in matrixes and on continuous surfaces, and very short subequal limbs in forms associated with dense low ground vegetation. Sexual dimorphism in limb proportions is found in some taxa, females having shorter and usually more equal limbs, but it is not known if this reflects differences in structural habitat. Proportions of limbs may vary considerably among close relatives as do their growth patterns, indicating that they may be easily modified by natural selection. Variation also occurs in the relative lengths of the femur and crus.

On open ground, long hind limbs can be effectively deployed and provide a high-gear system that contributes most locomotor thrust and produces high speeds. In dense ground vegetation etc. the forelimbs are probably used more and the short legs can be deployed effectively in confined spaces. Among matrix climbers, the same advantages can apply and in climbers as a whole the relatively short hind limbs provide low-gear thrust against gravity while the forelimbs also contribute and, in addition, prevent the foreparts falling away from steep surfaces.

The caudifemoralis muscle, which is the main retractor of the thigh, has its origin in the proximal tail with multiple heads attached mainly to the non-autotomic pygal vertebrae. the number of these vertebrae increases in advanced ground-dwellers and this may enhance effective size of the muscle and hence limb power. In many lacertids, the most posterior part of the muscle, which is slender, extends a short distance on to the autotomic vertebrae and may consequently be lost during tail shedding.

The complex movements of the hind limbs in ground-running lacertids are described including their effects in ameliorating the supposed problem of crural rotation. In the hind feet of open ground dwellers, the metatarsals and toes 1–4 increase in length, allowing the long claws which act like athlete's spikes to gain purchase over a broad area. At the end of a stride, ground lizards may rise on to the tips of toes 2–4 of a single foot, something permitted by robust phalanges and restrictions on mesial flexion at the toe joints; toe 5 is scarcely used and often miniaturised. The gait of lacertids varies according to the degree the crus and foot are extended forwards, providing a variable gear system that alters as the lizard gains speed; however on very steep surfaces climbing species rarely extend the leg fully.

In climbers on open surfaces, metatarsal 3 is longest allowing toe 3 to be deployed anteriorly or posteriorly. Toes are often spread broadly and a positive grip obtained by a system of digital kinking that allows them to shorten after claw insertion. While kinking is beneficial to climbing lizards, its exact pattern may be partly arbitrary and varies considerably across taxa. Slender phalanges and robust tendons reflect the fact that toes of climbing lizards are often under tension. Upward thrust is maximised by maintaining the grip of the feet as long as possible. This is facilitated by a system that allows differential flexion of the digits and by substantial flexibility of their joints.

The morphologies that facilitate each of these two contrasting kinds of locomotion place constraints on the other. Most ground dwellers have great difficulty ascending steep surfaces, while climbers do not rise on the tips of the hind toes when running on the ground. Feet of forms using dense ground vegetation and of matrix climbers have their own characteristics but respectively tend to resemble the two kinds described above. Many lacertids show some intermediacy in limb morphology that reflects the conflicts and compromises of moving in more than one type of habitat.

The mode of locomotion of the immediate ancestor of modern lacertids is unknown but some degree of climbing is widespread in the primitive Palaeoartctic assemblage, even though a number of ground forms also exist. In the Armatured clade some climbing appears to be primitive and there are clear shifts: to specialised climbing on open surfaces, to matrixes, to using dense ground vegetation and finally to open ground.

INTRODUCTION

Locomotion of lizards has recently become a fashionable area of enquiry, particularly locomotor performance and its relationship to the ecology and morphology of the forms concerned (see for instance summary by Garland & Losos, 1994). While performance has often been studied in detail and comparative ecology is frequently well understood, morphology has often been limited to simple measurements, especially hind limb length. Little has been written in this context about foot morphology and how this affects locomotion, the main exceptions being for specialised feet such as the adhesive pads of anoles and geckoes (see for example Russell, 1976).

The 230 or so species of lacertid lizards occupy a wide range of

structural niches and, although they are morphologically quite uniform in many respects, exhibit substantial variation in limb proportions and structure of the feet, features that are often used in systematics (see for instance Boulenger, 1920, 1921). Informal observations suggest that limb and foot differences confer performance advantages in locomotion in particular habitats. This probable correlation between structure and function is explored here, and phylogenetic information used to get some idea of historical shifts in habitat and morphological features important in locomotion. As will become apparent the topic as a whole has many aspects and ramifications, all of which are susceptible to detailed and rigorous exploration. The intention of this article is to provide a preliminary overview that will allow such investigations to be placed in a broad context.

PHYLOGENETIC RELATIONSHIPS OF THE LACERTIDAE

The successively distant outgroups of the Lacertidae appear to be the 1. the Teiioidea, consisting of the Teiidae and the Gymnophthalmidae; 2. the Scincoidea consisting of the Scincidae, Cordylidae, Gerrhosauridae and probably the Xantusiidae; 3. the Anguimorpha (Estes, De Queiroz & Gauthier, 1988; Gauthier, pers. comm.). Phylogenetic hypotheses within the family based on morphology have been discussed elsewhere (Arnold, 1989a) and some of these relationships have been modified and extended on the basis of investigations using mitochondrial DNA sequence (Harris, Arnold & Thomas, submitted a). The phylogenies of particular groups of lacertids have also been explored (Arnold, 1989b, 1991, 1997; Harris, Arnold & Thomas, in press, submitted b–d).

DNA evidence suggests that the most basal branch within the family may comprise the sister genera *Gallotia* and *Psammodromus*. There may then be a dichotomy into two large clades (Fig. 1), one consisting of relatively primitive mainly west Palearctic taxa the other of forms that possess a combination of a complex supporting structure in the hemipenis, the armature, and a usually derived ulnar nerve condition (Arnold, 1989a). This Armatured clade contains *Omanosaura* and all the Afrotropical lacertids and some morphologically derived genera found in the arid parts of the Saharo-Eurasian region (Fig. 2). While relationships within the Armatured clade are reasonably well resolved, largely on the basis of morphology, those in the primitive west Palearctic assemblage are less clear. This group can be referred to as *Lacerta* and its allies, and consists of a paraphyletic *Lacerta* from which is derived *Algyroides* and *Podarcis*. The east Asian *Takydromus* may be sister taxon to *Lacerta* and its allies but the evidence for this is not strong and for present its relationships to this group and the Armatured clade are best regarded as unresolved. A number of assemblages within *Lacerta* and its allies can be tentatively recognised (Fig. 1).

1. *Lacerta agilis* group: *L. agilis*, *L. bilineata*, *L. media*, *L. pamphylica*, *L. schreiberi*, *L. strigata*, *L. trilineata*, *L. viridis*
2. *L. lepida* group: *L. lepida*, *L. pater*, *L. princeps* and *L. tangitana*. This assemblage has often been associated with the *L. agilis* group on the basis of morphology (Boulenger, 1920; Arnold, 1973, 1989a) and, although immunological data do not suggest such a relationship, DNA sequence does give some admittedly weak support.
3. *Lacerta vivipara*.
4. *Podarcis* and its relatives *Lacerta andreanskyi* and the sister species, *L. dugesii* and *L. perspicillata*.
5. *L. saxicola* group, consisting of *Lacerta saxicola* and generally similar 'archaeolacertas' in the Caucasus area including *L. chlorogaster*, *L. derjugini* and *L. praticola*. *L. brandtii* may be related to this assemblage.
6. Northwestern 'archaeolacertas'. *Lacerta bonnali* and the similar *L. aranica* and *L. aurelioi*, *L. horvathi*, *L. monticola*, *L. mosorensis*.
7. *Algyroides*
8. Southern 'archaeolacertas': *L. bedriagae*, *L. cappadocica*, *L. danfordi* group (*Lacerta anatolica*, *L. danfordi*, *L. oertzeni*), *L. bedriagae*, *L. graeca*, *L. kulzeri*, *L. laevis* and *L. oxycephala*. Unlike the other groupings, there is no evidence that these species constitute a clade.
9. *L. parva* and *L. fraasii*. Although morphology suggests these forms may be related to *Psammodromus* and *Gallotia* (Arnold, 1989a), mtDNA sequence provides no support for this arrangement, suggesting instead a relationship to *L. danfordi*.

STRUCTURAL NICHES OF LACERTID LIZARDS

Overview of lacertid structural niche space

The spatial niches that lacertid lizards occupy differ in both microclimate and their structural properties (Arnold 1973, 1987). The main structural variables include the nature, continuity and angle of the surfaces on which the lizards are active. Essentially the range of structural niches occupied forms a continuum. Many species occur on open ground that is flat or gently sloping. The substratum may be gravel or small stones, earth or sand or some mixture of these. Sandy substrata may be firm, soft, or even the mobile slip faces of dunes. In some situations the ground may be entirely bare but there is frequently cover of varying density and patchiness, consisting of grass or other herbaceous vegetation, bushlets or bushes. Lizards may take refuge among such plants when disturbed and, when cover is more continuous, some forms may spend much time in the interstices of vegetation near the ground. The interstices among pebbles or small rocks constituting scree may be occupied in a similar way. Some lacertids regularly climb high among vegetation including the twiggy matrixes of bushes and tree canopies, or flimsy plant matter such as herbs or high grass, over the top of which some forms may run. In contrast, many species climb in a different kind of situation characterised by continuous sloping or vertical surfaces, for instance rock faces, large boulders and tree boles and branches.

Some lacertid species specialise in a relatively narrow and homogeneous section of the habitat continuum occupied by the family as a whole. Others may spend time in more than one part, for instance, *Podarcis muralis* occurs on occasion on bare ground and among low vegetation but also climbs in hedges, on boulders and rock faces and even tree boles. Similarly, *Psammodromus algirus* is cursorial on the ground but also climbs in dense often spiny vegetation.

Structural habitats occupied by groups within the Lacertidae

Few quantitative data exist on differences in structural niche between lacertid taxa, but less formal information is available for many forms. This is briefly summarised here. Citations often refer to summaries rather than scattered primary sources. Information on many west Palearctic taxa can be found in Böhme, 1981, 1984, 1986; Arnold, 1987 and Arnold & Burton, 1978). The notes on lacertid habitats by R.H.R. Taylor cited below were made in northern Somalia in the 1930s and are deposited in the archives of the Reptile Amphibian Section, Natural History Museum, London.

Taxa are discussed in the approximate order in which they appear on the estimates of phylogeny in Figs. 1 and 2.

Primitive Palearctic forms

Psammodromus (SW Europe, NW Africa)

P. algirus often occurs on the ground in dry vegetated places but, as noted, also climbs extensively in bushes etc. The three species that constitute the *Psammodromus hispanicus* clade are strictly ground dwelling usually in places with patches of low dense vegetation in which they take refuge.

Gallotia (Canary islands)

All species occur extensively on the ground but also climb effectively.

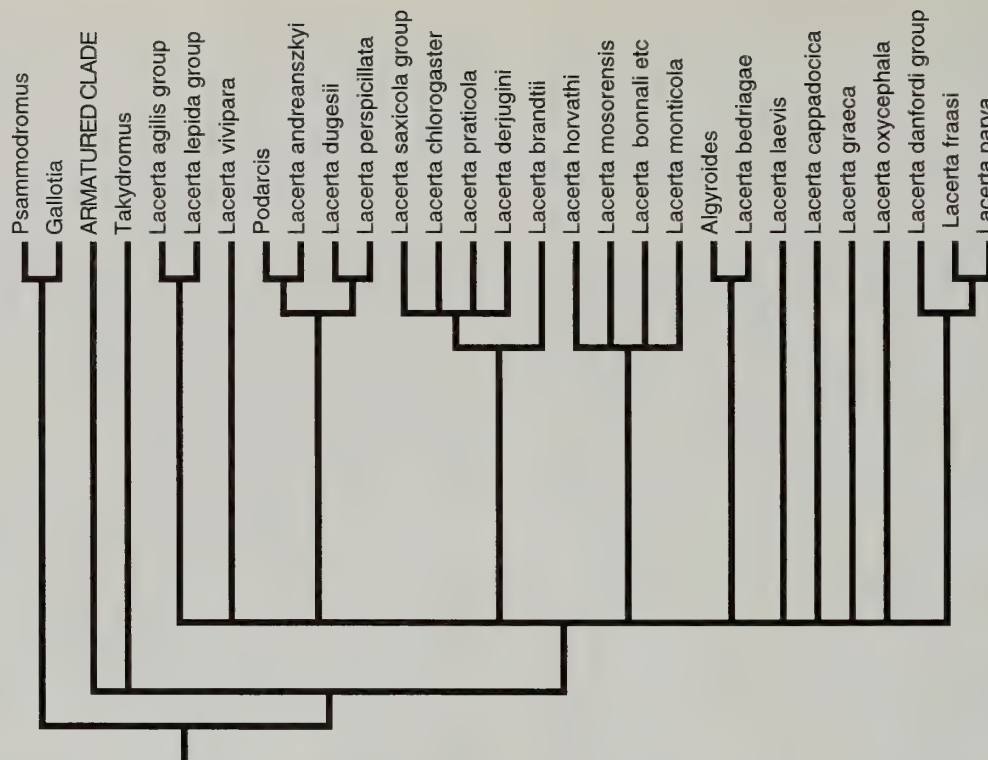


Fig. 1 Estimate of phylogeny for the Lacertidae. Relationships among many primitive Palearctic taxa are largely unresolved. For contents of assemblages within the paraphyletic genus *Lacerta* see p. 65. As it is shown here the *Lacerta saxicola* group is not a clade.

Takydromus (E Asia).

This genus is made up of two sister clades, the subgenera *Takydromus* and *Platyplacopus*, with *T. amurensis* either basal to both or basal within the subgenus *Takydromus* (Arnold, 1997). Basal species in the genus *Takydromus* tend to be mainly ground dwelling but in each of the two constituent clades there is progressive shift to extensive climbing in flimsy vegetation such as grass and herbs. However, various morphological features likely to give performance advantage in such situations occur throughout the genus, which suggests that it may have been ancestrally climbing. If so there may have been a shift to a more ground-dwelling life mode and then two reversions to climbing (Arnold, 1997).

Lacerta agilis group (Europe, SW Asia)

Ground-dwelling and climbing especially in brambles (*Rubus*) and similar vegetation. *L. agilis* is more ground dwelling than the other species.

Lacerta lepida group (SW Europe, NW Africa, SW Asia)

Ground dwelling and climbing.

Lacerta vivipara (Europe eastwards to Sachalien)

Ground dwelling in and around herbaceous and heathland vegetation.

Podarcis (NW Africa, S and central Europe)

P. hispanica, and *P. muralis* are frequently active on the ground but also climb extensively, especially on rocky surfaces. Other species of *Podarcis* climb to varying extents but usually less than most populations of *P. hispanica* and *P. muralis*, spending a larger proportion of time on or close to the ground. This trend is particularly apparent in such forms as *Podarcis sicula*, *P. melisellensis* and especially *P. taurica*. *P. sicula* often runs considerable distances

across open areas. (Sources: Böhme, 1986; Arnold, 1987; Arnold & Burton, 1978; pers. obs.).

Lacerta andreanskyi (Atlas mountains of Morocco)

This high altitude species has been observed on flat or gently sloping areas of scree with many interstices and often some vegetation (Busack, 1987; pers. obs.). It is active on the irregular surfaces of such situations but also spends considerable time travelling through the spaces between the stones, something that can be confirmed by providing captives with a similar structural environment. The lizards pass through very narrow gaps and also often make sharp turns in confined spaces. *L. andreanskyi* make use of the thermal properties of the scree column to maintain their body temperature when the sun disappears. At such times, they retreat into the layer of stones immediately below the surface which still retains heat, descending further into more secure refuges when these cool (pers. obs.).

Lacerta dugesii and *L. perspicillata* (Madeira, NW Africa)

Both these species climb to a considerable extent on open usually rocky surfaces, a trend that is better developed in *L. perspicillata* (pers. obs.).

Lacerta saxicola group (Caucasus area and adjoining north Iran, Iraq and Turkey)

Lacerta saxicola and generally similar species in the Caucasus and adjoining areas occur especially on rocky exposures of various kinds. *L. chlorogaster* of north Iran etc is distinctive in being found in forest where it climbs on tree boles, while *L. praticola* and *L. derjugini* are mainly ground dwelling in mesic herbaceous situations (Bannikov *et al.*, 1977; Darevskii, 1967; Lantz & Cyren, 1947).

L. brandtii, which may possibly be related to the *L. saxicola* group, is basically ground-dwelling occurring in dry, open though

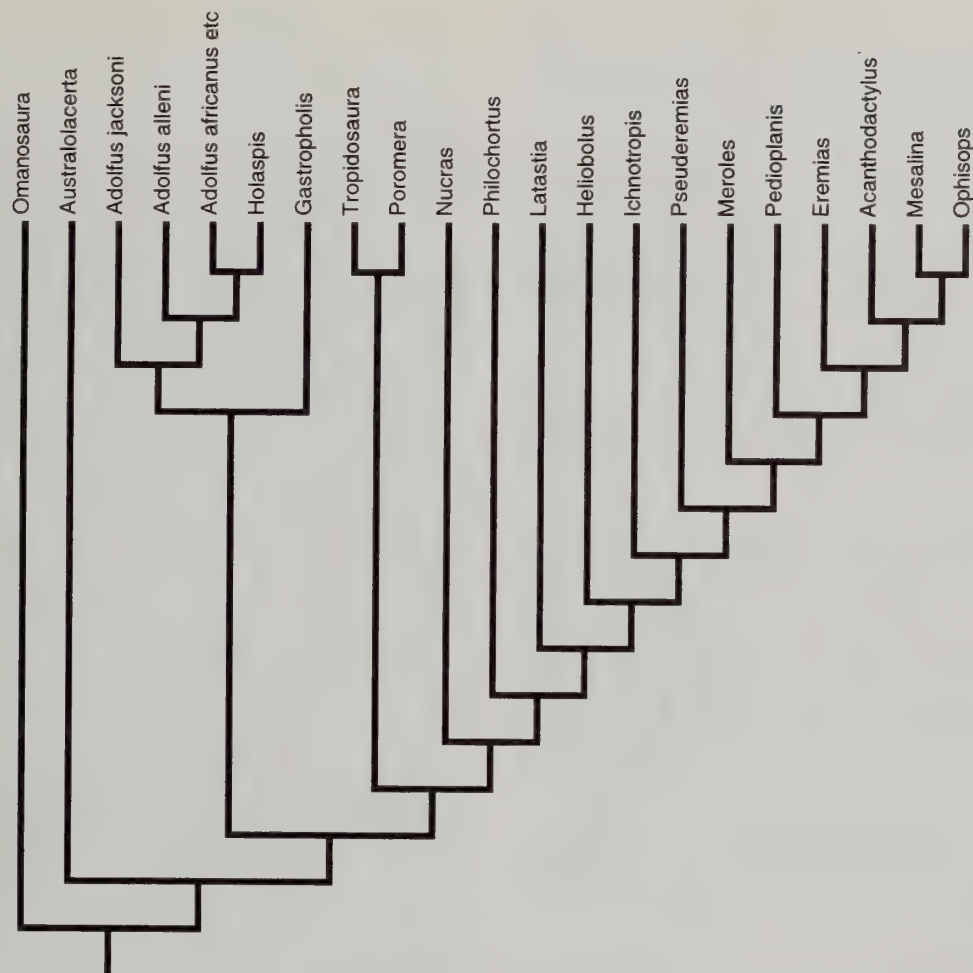


Fig. 2 Estimate of phylogeny for the Armatured clade of the Lacertidae. *Adolfus*, *Holaspis* and *Gastropholis* constitute the Equatorial African group.

sometimes broken situations with stones and sparse vegetation (Lantz & Cyren, 1939; S. C. Anderson, in press).

Northwestern archaeolacertas (NW Balkan area, S Austria, Pyrenees and Iberian Peninsula).

L. horvathi, *L. mosorensis* and *L. monticola* are rock dwelling in montane situations (Arnold, 1987) and the same is apparently true of *L. bonnali*, *L. aurelioli* and *L. aranica*.

Algyroides (S Europe)

This small genus appears to be primarily associated with woodland and woodland-edge habitats. In environments which have not been radically disturbed, *Algyroides* are frequently encountered among forest detritus such as fallen trunks, branches brushwood and litter. All four species may climb to some extent both in twiggy situations and on more continuous surfaces, including boles, branches and rocks. Such climbing is much more marked in *A. nigropunctatus* and *A. marchi* than in *A. fitzingeri* and *A. moreoticus* (Sources summarised by Arnold, 1987)

Southern 'archaeolacertas' (N and E Mediterranean area, east to N Iraq).

All species climb substantially although to varying extents. Climbing usually takes place on rocky surfaces (Arnold, 1973, 1987) but *L. laevis* sometimes also occurs on tree boles (Zinner, 1967). The most scansorial species is *L. oxycephala*. (Sources: Böhme, 1984; Arnold, 1987)

Lacerta parva and *L. fraasii* (Lebanon, E. Turkey, NW Iran, Transcaucasus)

Both species are basically ground-dwelling occurring in dry, open though sometimes broken situations with stones and sparse vegetation. (Wettstein, 1928; Peters, 1962; S. C. Anderson, in press; In den Bosch, 1994)

Members of the Armatured clade

Omanosaura (E Arabia)

Both *O. cyanura* and *O. jayakari* climb on rocky surfaces, but the latter species also spends time on open ground and occasionally even climbs in low trees (Arnold & Gallagher, 1977; pers. obs.).

Australolacerta (South Africa)

Both *A. australis* and *A. rupicola* occur on rocky surfaces and climb to a considerable extent (FitzSimons, 1943; De Villiers, Branch & Baard, 1983; Branch, 1988).

Adolfus (Forest regions of east and central Africa)

A. jacksoni, *A. africanus* and *A. vauereselli* are all essentially woodland species that often climb on fallen timber and sometimes standing trees as well. They also forage on the ground and *A. africanus* at least may climb twiggy and herbaceous plants (pers. obs.). *A. alleni* is a high altitude species occurring above the tree line in moorland situations where it lives on the ground, taking refuge in

dense tussocks of coarse and spiny vegetation. (Sources summarised by Arnold, 1989b).

Holaspis (Forest regions of tropical Africa and some adjoining savanna areas.)

The single species, *H. guentheri*, occurs on the trunks and branches of standing trees, often at some height, and does not usually come to the ground. It appears to spend much more time on steep and vertical surfaces than any other lacertid and also often investigates narrow crevices in wood and under bark. *Holaspis* is unique within its family in being able to glide from tree to tree. (Sources summarised by Arnold, 1989b).

Gastropholis (Forested areas of tropical Africa)

The little information available suggests the four species of this genus are arboreal and essentially canopy forms, spending much of their active time among twiggy vegetation. (Sources summarised by Arnold, 1989b).

Tropidosaura (S Africa).

These are ground-dwelling species in mountain areas and are usually encountered in and around dense grassy or bushy vegetation. Such behaviour occurs in the most basal species of the clade, *T. montana*, and may be primitive for the genus, all members of which lack a collar beneath the throat and have large imbricate, pointed, keeled dorsals, features usually associated with use of dense vegetation as cover (Arnold, 1973). Two of the four species, *T. gularis* and *T. cottrelli*, also climb on rock surfaces to a limited extent. If this is a derived condition it is likely to have developed twice. (Sources: Branch, 1988, pers. comm.; pers. obs.).

Poromera (Forested areas of W Africa from Gabon to Cameroun.) Occurs on the forest floor and on fallen logs (M. Largen pers. comm.; Freyhoff, 1994) and also climbs in grassy vegetation (Perret and Mertens, 1957).

Nucras (E and southern Africa)

Ground dwelling especially in mesic and arid savannah often on sandy soils. Many species are secretive and only seen after rain, although *N. tessellata* is active at high temperatures. *N. lalandei* occurs under stones and in long grass. (Sources: Branch, 1988, pers. comm.; FitzSimons, 1943; Pianka, 1986).

Philochortus (NE Africa; isolated localities in and around the Sahara desert)

Ground dwelling in dry places on sandy and stony soils often with grass and bushes (R.H.R. Taylor, notes). Matschie (1893) recorded *P. neumanni* from high grass. *Philochortus* possesses morphological features that have independently evolved in the lacertid genera that climb in grassy vegetation, *Takydromus* and *Poromera*, and appear to confer performance advantage in that situation; these features include, enlarged vertebral scales with a coarse microornamentation of anastomosing ridges, a long tail and sagittally expanded neural spines (Arnold, 1997).

Latastia (SW Arabia, NE and E Africa, westwards through the Sahel)

Ground dwelling in dry places with sparse vegetation (Dunger, 1967; R.H.R. Taylor, notes; J. Vindum, pers. comm.).

Heliobolus East and tropical southern Africa, Sahel etc.)

Ground dwelling in dry places. *H. lugubris* occurs on sparsely vegetated compacted sandy plains and in bush veldt (Branch, 1988; FitzSimons, 1943; R.H.R. Taylor, notes).

Ichnotropis (Tropical southern Africa)

Ground dwelling in arid and mesic savannah often with sandy soil (Branch, 1988; FitzSimons, 1943).

Pseuderemias (NE Africa)

On dry ground ranging from firm, rocky substrata to dunes (Gans & Laurent, 1965; R.H.R. Taylor, notes).

Meroles (SW Africa)

The evolution of this arid ground-dwelling clade is discussed elsewhere (Arnold, 1990, 1991) and habitat differences between the species summarised (Arnold, 1995). Most species occur on sandy substrata but a succession of shifts to increasingly extreme environments occur along the main lineage of the phylogeny. The sequence is: relatively firm surfaces (*M. knoxii* and *M. suborbitalis*), vegetated hummocks separated by open areas of soft sand (*M. reticulatus*), areas of looser sand and more open vegetation (the subgenus *Saurites*, consisting of *M. ctenodactylus*, *M. micropholidota* and *M. cuneirostris*), bare slip faces of dunes (*M. anchietae*). Overall the trend is towards softer substrata and more open situations.

Pedioplanis (S Africa and Namibia)

Ground dwelling in dry usually open areas on firm substrata such as flat and sloping rocky areas, gravel, hard soils, sandy plains and grassy hillsides (FitzSimons, 1943, Branch, 1988).

Eremias (Palearctic Asia and adjoining regions)

Ground dwelling in dry situations and habitats occupied by members of the genus include firm soil, firm sand, loess and aeolian sand; the latter habitat may have been entered twice (S. C. Anderson, in press; Minton, 1966; Shcherbak, 1974; Smith, 1935).

Acanthodactylus (N Africa, Middle east to NW India)

Ground dwelling in open dry situations, usually on light soils or sand. Within this general environment, there is considerable variation in microhabitat among species. Many relatively primitive forms usually occur on fairly firm substrata with at least scattered vegetation and the *A. pardalis* group is found on loess soils. Perhaps three lineages appear to have shifted into aeolian sand habitats, although they may sometimes have partially reverted to firmer ground: 1. *A. grandis* of Syria, Iraq and adjoining regions; 2. the *A. scutellatus* clade of North Africa and northern Arabia of which *A. longipes* is found in the softest most open situations (Perez Mellado, 1992; S. Baha el Din, pers. comm.); 3. a clade ranging from Arabia to NW India consisting of *A. cantor* and its immediate relatives, among which *A. haasi* is distinctive in often climbing in bushes. (Sources: S. C. Anderson, in press; Arnold, 1983, 1984, 1986a; Dunger, 1967; Ross, 1989, Mellado & Olmedo, 1991; Perez Mellado, 1992)

Mesalina (N Africa, Arabia, Middle East to NW India)

Ground dwelling in dry, open situations on firm substrata. Most species tend to occur on compact often sandy soils but members of the clade containing *M. guttulata* and *M. watsonana* are often found in gravelly, stony or rocky situations. (S. C. Anderson, in press; Arnold, 1984; Minton, 1966; Perez Mellado, 1992; Ross, 1989).

Mesalina ercolinii (Lanza and Poggesi, 1975) is only known from a single specimen collected in central Somalia. It was initially assigned to *Eremias* but is probably part of the *Mesalina* clade (Arnold, Lanza *et al.*, in press). The sole individual was collected in a savannah habitat but there are no direct observations on its life mode.

Ophisops (Coastal regions of N Africa; Turkey and Middle east to India and Sri Lanka)

Ground-dwelling, usually in generally dry situations often on sandy soils which may bear grass or patches of dense vegetation. (S. C. Anderson, in press; Minton, 1966; Schätti & Gasperetti, 1994; Smith, 1935). In Sri Lanka, *O. leshchenaultii* occurs in more open dune areas (T. B. Karunaratne, pers. comm.).

Evolutionary change in structural niche

Because of the range of habitats occupied by lacertids and the wide variation in degree of climbing they exhibit, it is very difficult to assign species to a simple set of well defined structural niche states. However there are a number of broad categories that can be recognised, even though there is considerable variation within these and some species may be assignable to more than one.

G – Ground dwelling in open areas.

V – Ground dwelling and spending considerable time in situations where movement may be restricted, such as dense grassy or twiggy vegetation and the analogous interstices of scree etc.

M – Climbing regularly in vegetation where the lizard tends to progress through or over a matrix of twigs, leaves or grass.

C – Climbing regularly on more or less continuous largely open surfaces, such as rock faces and tree boles.

The immediate outgroup of the Lacertidae, the Teiioidea, is almost entirely ground dwelling and this appears to be the primitive situation for the next most closely related outgroups, the Scincomorpha and the Anguimorpha. However, while this suggests the earliest lacertids may have been ground dwelling too, this is not necessarily so for the immediate ancestor of surviving species.

Unfortunately, the overall history of structural niche within the family is difficult to assess because basal relationships within the primitive Palaearctic assemblage are not fully resolved. However many of the component taxonomic units of this assemblage include species that climb to some extent and often, taking these units on their own and considering all evidence, it is more parsimonious to regard some degree of climbing as the primitive situation relative to a more ground-dwelling life mode. This is true for instance in *Takydromus*, *Podarcis* and its relatives and the *Gallotia*-*Psammadromus* clade.

Whether it is assumed ground dwelling or climbing is primitive for the surviving members of the family, numerous transitions between different kinds of structural habitats have to be postulated. Even within *Takydromus* there may have been a shift from climbing to a more ground dwelling way of life and then two independent shifts back to climbing (p. 66).

When some degree of climbing versus ground-dwelling is plotted on the general pattern of relationships assumed here for the primitive Palaearctic assemblage, it is more parsimonious to assume some degree of climbing as the initial state, with multiple shift to life mainly on the ground, either in and around dense vegetation or in more open situations. However, this assumption is not very robust, as assuming a ground-dwelling ancestry in *Takydromus* rather than a climbing one makes the ancestral condition uncertain.

If a partially climbing ancestry is accepted, there must have been, within the primitive Palaearctic assemblage, shifts to more specialised climbing on continuous surfaces (C) in such forms as *Lacerta oxycephala* and *L. perspicillata*, and to specialised climbing in vegetation matrices (M) in *Takydromus*. *L. vivipara* would have become ground-dwelling in dense vegetation (V) and this would have occurred separately in *L. derjugini* and *L. praticola* within the *L. saxicola* group. The *L. parva*-*L. fraasii* clade and *L. brandtii* would have separately entered more open ground situations (G), and the *Psammadromus hispanicus* clade occupied often intermediate habitats (G and V).

The history of alteration of structural niche is clearer in the Armatured clade where phylogenetic structure is more apparent. Here, some climbing on continuous surfaces appears to have been the primitive situation. In the Equatorial African group there was one shift to specialised open surface climbing (C) in *Holaspis*, one to matrix climbing (M) in canopy in *Gastropholis* and one to using

ground vegetation (V) in *Adolfus alleni*. In the main lineage of the Armatured clade, parsimony supports a shift to more extensive ground dwelling in the ancestor of the clade made up of *Tropidosaura* and its advanced relatives with subsequent shift to more open habitats. At the base of this clade there would have been partial shifts to other modes: a reversion to a small degree of climbing in two species of *Tropidosaura*, and to making some use of vegetable matrixes in *Poromera* and perhaps *Philochortus*. Alternatively, *Tropidosaura*, and *Nucras* and its advanced relatives may have become ground-dwelling independently.

Overall there may have been a minimum of nine shifts to ground dwelling although only about three were into really open situations (G), five to climbing in vegetable matrixes and others to specialised climbing on continuous surfaces. Among members of the Armatured clade, there were multiple shifts on to soft sandy substrata: at least one each in *Pseuderemias*, *Meroles* and *Eremias* and perhaps three in *Acanthodactylus*.

Reversals in structural niche within the Lacertidae are less obvious, although morphology suggests this may have happened in *Takydromus*, *Acanthodactylus* and *Meroles*.

MORPHOLOGY

Body proportions and vertebral number

Bodies of lacertids vary in their proportions, especially in the extent of elongation, and change in number of presacral vertebrae is often associated with this. The number shows some individual variation in most species and females usually have more presacral vertebrae than males (often about one on average but sometimes two). Typically there are eight nuchal vertebrae and five sternal vertebrae with ribs attached to the sternum, but the number of more posterior presacral vertebrae varies considerably. There may be as few as ten in some *Pseuderemias* and *Acanthodactylus* and as many as twenty in some female *Nucras lalandei*, making the total presacral range for the family 23 to 33 vertebrae.

Fairly elevated presacral counts also occur in *Lacerta agilis*, *Lacerta parva* and *L. fraasii*, some members of the *L. saxicola* group, *L. andreanskyi*, *L. graeca*, *Adolfus alleni* and *Gastropholis* (Arnold, 1973, 1989b). Females of these forms often have a total of 29 presacral vertebrae while *Gastropholis* frequently possesses 30. Relatively low presacral counts of 24 to 26 in females are usual in the more derived members of the Armatured clade including *Philochortus* and its sister group; they also occur sporadically elsewhere.

Presacral vertebral count shows some correlation with habitat. Forms where it is high include those that spend time in dense vegetation, such as *Lacerta agilis*, *Adolfus alleni*, *Gastropholis*, and *Nucras lalandei* while numbers are particularly low in species regularly occurring in open situations. This may be related to the amount of body flexibility necessary to negotiate habitats where possible paths are often tortuous and ones which are unimpeded. *L. andreanskyi* which may spend considerable time in the interstices of scree also has high counts. However any association between vertebral number and the functional demands of habitat is imprecise, as high counts also occur in forms that often live in open rocky situations, such as *Lacerta graeca* and members of the *L. saxicola* group.

Sexual variation in presacral vertebral count is absent in *Gallotia*, and independently lost three times in *Acanthodactylus*: in *A. bedriagai*, in *A. schmidtii* populations in the United Arab Emirates, and in the *A. scutellatus* group. All these cases appear to involve reduction in female presacral number, except *A. bedriagai* where

there may have been an increase in male counts. In several ground dwellers in dense vegetation, females have on average two more presacral vertebrae than males. Included here are the *Psammodromus hispanicus* group, *Lacerta agilis*, *L. derjugini*, *L. praticola*? and *Adolfus alleni*. Number of abdominal vertebrae appears also to be influenced by relative clutch mass (Bauwens, Barbadillo & Gonzalez, 1997).

Relative tail length

Because caudal autotomy and partial regeneration are frequent, adequate data on the relative length of intact tails in adult lacertids are not easy to collect. In most adult lacertids, intact tails vary in length from about 1.7 to about 2.7 times the length of the head and body. However, they are often over three times as long in many *Takydromus*, *Psammodromus algirus*, *Gastropholis*, *Philochortus neumanni* and *P. hardeggeri*, *Latastia longicaudata*, *Pseuderemias mucronata* and *P. striata*. The longest tails occur in *Takydromus sauteri*, where they

may be four times as long as the head and body, and in some *T. sexlineatus*, where the tail is five times as long. Tails are particularly short, being around 1.4 to 1.6 times the head plus body length, in *Holaspis*, *Eremias argus*, *E. przewalskii*, *E. quadrifrons*, *Acanthodactylus tristrami*, *A. robustus* and *Mesalina rubropunctata*. In *Meroles anchietae* and *Eremias arguta* the figure falls to about 1.

Very long and very short tails are both derived conditions within the Lacertidae that have arisen several times. Very long tails are frequent in forms that climb in vegetation matrixes, such as *Takydromus*, *Gastropholis*, *Psammodromus algirus* and perhaps the species of *Philochortus* mentioned. In at least the first two genera, the tail is used to maintain position among stems and twigs (Arnold, 1989b, 1997) and, in general, appears to spread weight in flimsy vegetation. This occurs in some *Takydromus*, such as *T. sexlineatus*, when they run across the top of high grass, a situation where the tail may perhaps also contribute thrust through lateral sinusoidal motion. In the two main clades of *Takydromus* (Arnold, 1997) there are

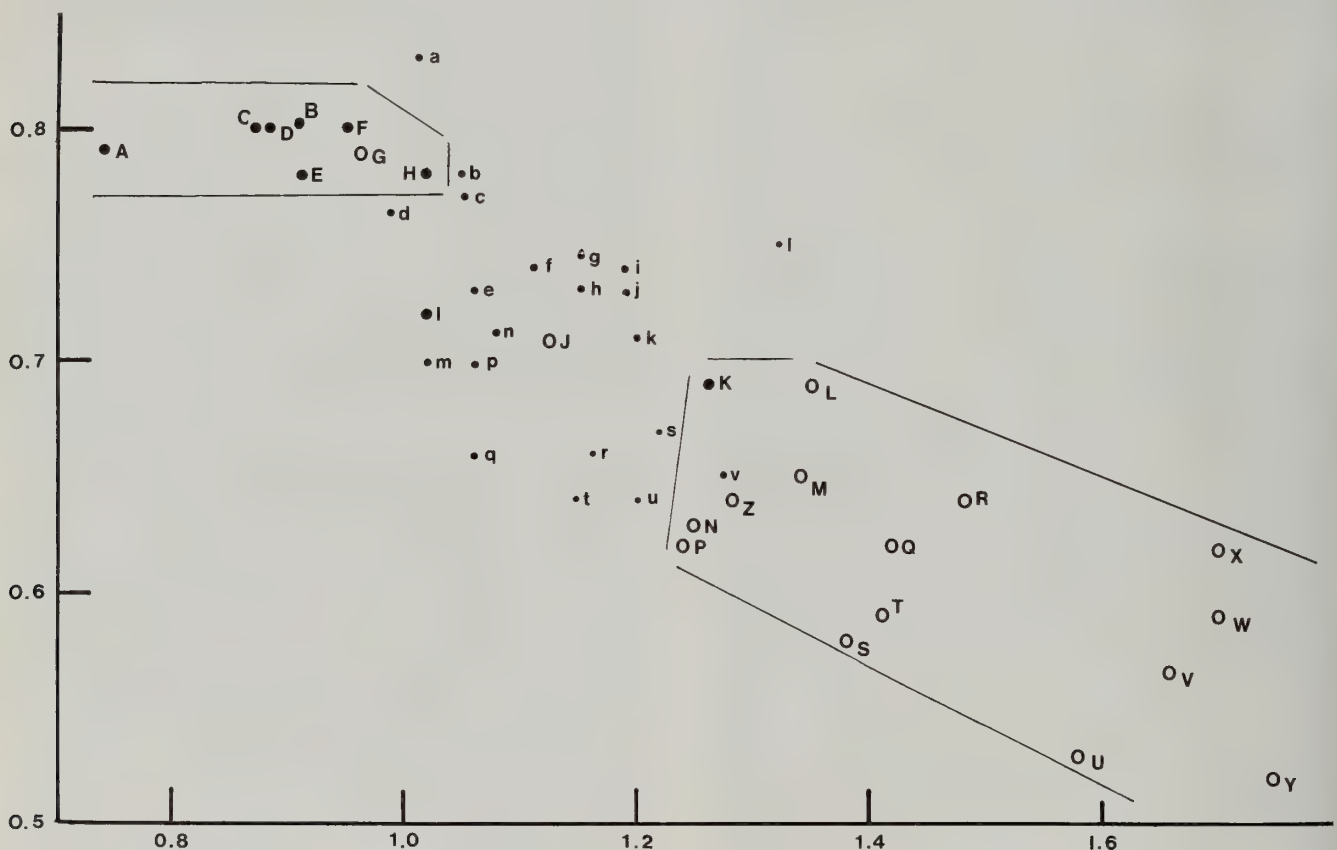


Fig. 3 Limb proportions of lacertid lizards based on data in Table 1; sexes pooled. Vertical axis: FL/HL – Forelimb span/hindlimb span. Horizontal axis: HL/SV – Hindlimb span/snout-vent distance. ● – More primitive ground dwellers; ○ – Ground dwellers of the clade consisting of *Philochortus* and its sister group; ◐ – forms that regularly climb to some extent. Ground dwellers using dense vegetation (upper box), also included is *Lacerta andreanskyi* which often occurs in the interstices of scree: A. *Nucras lalandei*, B. *Lacerta vivipara*, C. *Lacerta andreanskyi*, D. *Tropidosaura montana*, E. *Adolfus alleni*, F. *Lacerta agilis*, G. *Mesalina ercolinii* and H. *Takydromus amurensis*. Ground dwelling forms of generally open situations (lower box): K. *Psammodromus hispanicus*, L. *Eremias persica*, M. *Ichnotropis capensis*, N. *Philochortus intermedius*, P. *Latastia longicaudata*, Q. *Ophisops schlueteri*, R. *Pedioplanis lineocellata*, S. *Acanthodactylus schmidtii*, T. *Acanthodactylus scutellatus*, U. *Heliobolus lugubris*, V. *Meroles reticulatus*, W. *Meroles ctenodactylus*, X. *Meroles anchietae*, Y. *Pseuderemias mucronata*, Z. *Mesalina balfouri*. Ground dwellers that probably fall between the above two situations: I. *Nucras boulengeri*, J. *Mesalina* species A, SW Arabia (Arnold, 1986b). Forms known to climb on continuous surfaces and in vegetation matrixes; overall, q–u appear to climb least: a. *Holaspis guentheri*, b. *Takydromus septentrionalis*, c. *Gastropholis vittata*, d. *Gastropholis echinata*, e. *Lacerta perspicillata*, f. *Lacerta pater*, g. *Lacerta oxycephala*, h. *Lacerta mosorensis*, i. *Lacerta jayakari*, j. *Algyroides nigropunctatus*, k. *Lacerta bedriagae*, l. *Poromera fordii*, m. *Podarcis hispanica*, n. *Podarcis muralis*, p. *Lacerta viridis*, q. *Podarcis melisellensis*, r. *Podarcis sicula*, s. *Lacerta laevis*, t. *Podarcis peloponnesiaca*, u. *Lacerta trilineata*, v. *Psammodromus algirus*.

independent shifts to increased climbing in vegetation and this is associated with greater tail length.

Apart from locomotory considerations, tail length in lacertids may be influenced by different patterns of predation associated with particular kinds of habitat. It has been suggested that long tails are more likely to be effective in deflecting the attack of ambushing predators and so would be expected in lizards that often hunt actively in complex spatial habitats where such predators might hide; in contrast it is predicted that more passively hunting lizards in open situations would have short tails. Some indications of such an association has been suggested for Southern African desert lacertids (Huey & Pianka, 1981) and, taking the family as a whole, nearly all species with very short tails are ground-dwellers in open situations. The only exception is the aberrant tree-dwelling and gliding *Holaspis*.

The pattern of tail growth varies in lacertids. Relative tail length often increases with body size, for instance in *L. dugesii*, *L. vivipara* and *L. jayakari*, but decreases in *Acanthodactylus scutellatus*. In *Lacerta lepida* relative tail length rises steeply at first but subsequently levels out and eventually tends to fall and a similar growth pattern appears to be present in *L. trilineata*

Limb proportions and structural niche

Limbs of lacertids are often measured individually (see for instance Darevskii, 1967), but in intact animals it is difficult to determine a reliable reference point for the base of the limb which is situated in soft tissue. Because of this it is easiest to measure the total span of a pair of limbs when fully outstretched, from the tip of the longest digit on one side to that on the other. Fore and hind limb spans can then be compared with each other and with the total length of the head and body measured from the tip of the snout to the vent. The latter is of course not an absolute criterion for comparison. As already noted, presacral vertebral number varies between species and sexes, and this is also true of the size of the head relative to the body; both these factors affect body length.

Estimates of hind leg span in terms of head and body length, and the ratio of foreleg and hind leg spans, are given for a wide variety of lacertids in Table 1 and the relative distribution of selected species in terms of these parameters is shown in Fig. 3. In the latter, the species all fall in a restricted area of the diagram. Not only do no forms exist where the forelimbs are longer than the hindlimbs but there is a broad correlation between hindlimb length and the relative length of the forelimbs: in cases where hindlimbs are comparatively short, forelimbs tend to approach them in length, but where hindlimb span is large, forelimb span is relatively much smaller. It follows from this that the overall range of hindlimb span in terms of body length is much greater than that of the forelimbs: for the former, the highest ratio is about 2.8 times the lowest compared with less than 1.5 times for the latter.

The kind of structural habitats species occupy correlates quite clearly with limb proportions. Ground dwelling forms that often occur in dense vegetation or litter have short, subequal limbs and this is true of *Lacerta andreanskyi* which appears to often spend time in the confining interstices of scree. Climbing forms are similar in proportion of the limb pairs although their legs are usually rather longer and this pattern is found both in climbers on open surfaces such as *Holaspis* and in forms from vegetation matrixes such as *Gastropholis* and *Takydromus*. Limbs are longer still in climbing forms that also utilise less steep surfaces quite extensively, such as *Lacerta oxycephala*. Forms which climb considerably but also run in more or less horizontal situations have even longer and less equal limb pairs. Species that scarcely climb and occupy open ground habitats all have very long hind legs and short front ones. This is best

Table 1 Limb proportions of lacertid lizards. HL/SV – Hindlimb span/snout-vent distance; FL/HL – Forelimb span/hindlimb span; m – male, f – female.

Species and sample size	HL/SV		FL/HL	
	Male	Female	Male	Female
Takydromus amurensis (6m,4f)	1.02	1.03	.78	.77
Takydromus septentrionalis (11m,10f)	1.08	1.02	.78	.77
Gallotia atlantica (3m,3f)	1.25	1.13	.69	.70
Gallotia g. caesaris (3m,3f)	1.34	1.26	.69	.69
Psammmodromus algirus (6m,6f)	1.30	1.24	.65	.64
Psammmodromus hispanicus (7m,10f)	1.30	1.23	.68	.70
Lacerta vivipara (10m,10f)	0.99	0.81	.82	.78
Lacerta agilis bosnica (10m,10f)	1.01	0.88	.80	.80
Lacerta viridis (10m,10f)	1.09	1.03	.70	.69
Lacerta trilineata (9m,10f)	1.20	1.20	.64+	.64
Lacerta lepida (5m,6f)	1.14	1.04	.71	.72
Lacerta pater (7m,5f)	1.11	1.10	.74	.73
Lacerta andreanskyi (1m,4f)	0.96	0.78	.73	.86
Lacerta laevis (10m,10f)	1.26	1.17	.66	.67
Lacerta danfordi (7m,5f)	1.27	1.16	.67	.68
Lacerta bedriagae (8m,13f)	1.23	1.16	.71	.70
Lacerta mosorensis 10m,10f)	1.17	1.1	2.71	.74
Lacerta oxycephala (10m,10f)	1.17	1.13	.74	.73
Algyroides nigropunctatus (10m,7f)	1.25	1.12	.71	.74
Lacerta perspicillata (9m,11f)	1.13	1.00	.72	.74
Podarcis hispanica (9m,6f)	1.18	1.05	.69	.71
Podarcis m. fiumana (10m,10f)	1.14	0.99	.65	.67
Podarcis muralis (10m,10f)	1.12	1.03	.71	.71
Podarcis s. campestris 10m,10f)	1.20	1.12	.66	.65
Podarcis peloponnesiaca (19m,11f)	1.20	1.09	.63	.64
Lacerta jayakari (7m,9f)	1.20	1.18	.75	.72
Adolfus alleni (9m,7f)	0.94	0.87	.77	.78
Holaspis guentheri (3m,4f)	1.01	1.01	.85	.80
Gastropholis echinata (4m)	1.05		.77	
Gastropholis tropidopholis (1f)		1.16		.74
Gastropholis vittata (1m,1f)	1.01	0.94	.76	.78
Gastropholis prasina (1m)	1.04		.77	
Tropidosaura montana (3m)	0.88		.8	
Tropidosaura gularis (1m,1f)	1.15	0.97	.72	.77
Tropidosaura essexi (2m)	1.05		.71	
Tropidosaura cottrelli (1m)	1.06		.77	
Poromera fordii (3m,3f)	1.35	1.28	.75	.74
Nucras boulengeri (7m,7f)	1.03	1.01	.72	.71
Nucras lalandei (4m,1f)	0.82	0.67	.79	.79
Philochortus intermedius (5m,4f)	1.34	1.16	.60	.66
Latastia longicaudata (10m,6f)	1.29	1.18	.61	.63
Heliobolus lugubris (7m,4f)	1.58	1.57	.53	.53
Ichnotropis capensis (9m,5f)	1.38	1.29	.64	.65
Pseuderemias mucronata (12m,6f)	1.81	1.68	.51	.53
Meroles reticulatus (1m,4f)	1.73	1.58	.60	.57
Meroles ctenodactylus (3m,1f)	1.7	1.7	.60	.58
Meroles cuneirostris (1f)		1.61		.57
Meroles anchietae (2m,1f)	1.74	1.66	.62	.62
Pedioplanis lineocellata (4m,4f)	1.49	1.46	.64	.64
Eremias persica (3m,5f)	1.38	1.32	.68	.69
Acanthodactylus schmidtii (12m,10f)	1.37	1.38	.58	.58
Acanthodactylus scutellatus (10m,3f)	1.42	1.41	.58	.59
Mesalina balfouri (6m,4f)	1.34	1.22	.63	.64
Mesalina 'A', SW Arabia (2m,4f)	1.20	1.04	.69	.72
Mesalina ercolini (1f)		0.96		.79
Ophisops e. schlueteri (5m,6f)	1.51	1.32	.62	.61

developed in *Latastia* and its sister group in the Armatured clade and reaches its extreme in forms like *Heliobolus lugubris*, *Pseuderemias mucronata* and the most derived species of *Meroles*. Among the species investigated here, advanced armatured ground dwellers are approached most closely in limb proportion within the primitive Palaearctic assemblage by *Psammmodromus*, the species of *Podarcis* that climb least, and by *Lacerta trilineata*.

Because of their correlation with spatial niche, limb proportions

can be used to generate hypotheses about the habitats and locomotory modes of species where these are uninvestigated or incompletely so. Thus the one known specimen of *Mesalina ercolinii* occurs in the area of Fig. 3 mainly occupied by ground dwelling forms using dense vegetation, an exceptional habitat for an advanced armatured lacertid. The African *Poromera fordii* has many morphological resemblances to the east Asian grass lizards, *Takydromus*, that seem to be related to climbing in vegetation (Arnold, 1997) but, although the limb pairs of *Poromera* are not very disparate in length, as expected in a climber, they are distinctly longer than in *Takydromus* and other scansorial species. This suggests a locomotory difference between the two genera and perhaps indicates that, although *Poromera* does climb in vegetation, it is also frequently active in open situations, for instance it may run on the ground more extensively than *Takydromus*.

Sexual dimorphism in limb length

It will be seen from Table 1 that there is sexual variation in relative length of the hindlimbs, which nearly always appear to be shorter in females. In most cases the apparent difference is slight, but in a number of taxa, it is substantial, the mean adult male hindlimb span in terms of body length sometimes being as much as 12% more than that of females. Marked sexual difference occurs in, among others, *Psammodromus hispanicus*, *Lacerta agilis*, *L. lepida*, *L. andreanszkyi*, *L. laevis*, *L. danfordi*, *Algyroides nigropunctatus*, *Lacerta perspicillata*, *Adolfus alleni*, *Podarcis*, *Philochortus intermedius*, *Latastia longicaudata*, *Pseuderemias mucronata*, *Mesalina* and *Ophisops*. In many cases, reduced hind limb span in females is associated with raised forelimb/hindlimb ratio, so sexual differences

within species follow the general trend among species (Fig. 4). There appear however to be exceptions to this regularity, for instance in *Lacerta vivipara*.

The sporadic distribution of marked sexual difference in limb length indicates that it has arisen a number of times. There are also phylogenetic indications that sexual dimorphism may have often developed by change in limb proportions of the females rather than the males.

The clear relationship among species between limb proportions and the kind of spatial niche occupied suggests that intraspecific sexual differences in limb length may reflect differences between the sexes in microhabitat, although these do not seem to have been systematically looked for. In some cases limb dimorphism is often associated with differences in dorsal colouring and pattern that may possibly be related to the problems of camouflage in different environmental situations. Thus, in *Podarcis*, females not only have shorter hind legs but are more obviously longitudinally striped than males, a pattern that may be more cryptic in more vegetated situations.

Many forms with sexual dimorphism in limb length also show dimorphism in head size which is probably associated with male combat for territory and females, large heads presumably conferring advantage in this situation. It might be thought that large limbs would also be beneficial in this context, but the relationship between head and limb size is not precise and some forms where the males have large heads show little apparent limb difference between the sexes, for instance *Lacerta viridis* and *L. trilineata*. The fact that sexual dimorphism in limb proportions may be produced by devia-

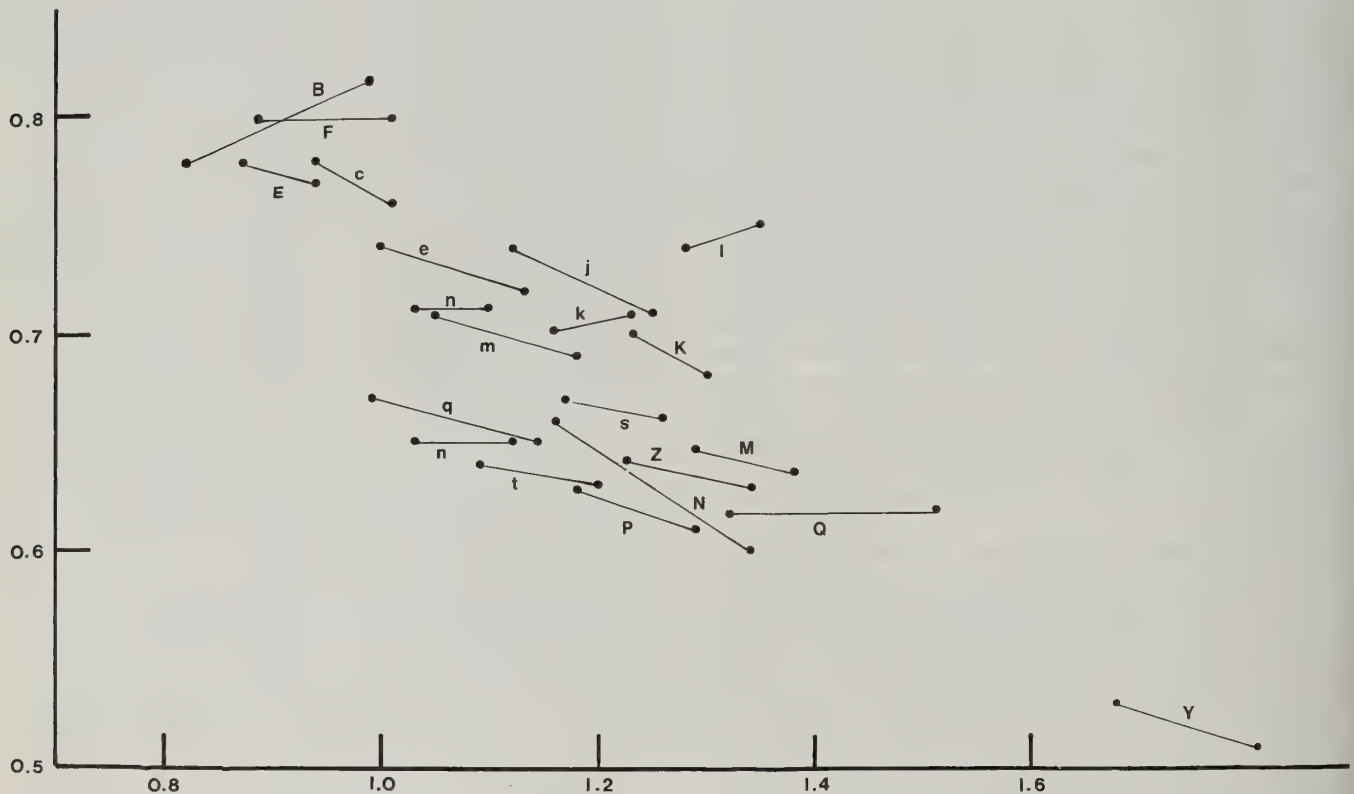


Fig. 4 Sexual differences in limb proportions in selected dimorphic species. Vertical axis: FL/HL - Forelimb span/hindlimb span. Horizontal axis: HL/SV - Hindlimb span/snout-vent distance. Lines join means for the two sexes, females are always to the left. Letters refer to species as indicated in the caption of Fig. 3. Sexual differences in hindlimb length are often large, compared with mean species differences; females often have more equal limb pairs than males.

tion to shorter limbs in females rather than increase in limb size in males also militates against this explanation.

It might be thought that the relatively low hindlimb/snout-vent ratios of many female lacertids is a result of their usually higher average number of presacral vertebrae than males (Arnold, 1973, 1989a), something that tends to produce a proportionally longer body. However, while this may be a partial cause of low ratios, it is not a total explanation. In *Gallotia atlantica* and *G. galloti caesaris*, for instance, where virtually all individuals have 26 presacral vertebrae without sexual difference, females still have relatively shorter hind legs.

Relative proportions of femur and tibia

Measurements of the femur and tibia on dry skeletons and cleared and stained preparations of single individuals of a wide range of lacertid species show considerable variation. The approximate ratio of tibia length to femur length is generally low in members of the primitive Palearctic assemblage and more basal members of the Armatured clade where it ranges from about 0.73–0.87. The ratio is particularly low, about 0.73–0.77, in such climbing forms as *Lacerta oxycephala*, *L. bedriagae*, *L. horvathi*, *L. perspicillata*, *L. mosorensis* and *Holaspis guentheri*.

Generally rather higher ratios, 0.76–0.87 occur in *Takydromus septentrionalis*, *Lacerta agilis*, *L. vivipara*, *Psammodromus algirus*, *Lacerta schreiberi*, *L. pater*, *L. chlorogaster*, *L. monticola*, *L. dugesii*, *Podarcis bocagei*, *P. muralis*, *P. sicula*, *Adolfus jacksoni* and *Poromera fordii*.

Ratios are higher still, 0.88–1.00, in *Psammodromus hispanicus*, *Lacerta trilineata*, *Adolfus alleni* and the clade containing more advanced members of the Armatured group, namely *Nucras* and its sister group, most of which are largely or entirely ground dwelling in open places. Included here are *Poromera fordii*, *Nucras boulengeri*, *N. lalandei*, *Philochortus spinalis*, *Latastia longicaudata*, *Heliobolus lugubris*, *Ichnotropis squamulosa*, *Pseuderemias brenneri*, *Meroles knoxii*, *M. ctenodactylus*, *Eremias arguta*, *Acanthodactylus erythrus*, *A. boskianus*, *Mesalina rubropunctata*, *Ophisops elegans*.

Patterns of limb growth

Like patterns of tail growth, the way in which the length of hind limbs relative to that of the head and body changes during growth from hatching to maturity is extremely varied. In such forms as *Takydromus septentrionalis* and *Lacerta oxycephala* the hindlimbs retain much the same relative size, while in *Acanthodactylus scutellatus* and *A. schmidtii* they show distinct reduction, for instance growing only 90% as fast as the head and body length in *A. schmidtii*. In *Podarcis hispanica* and *P. peloponnesiaca*, the relative length of the hindlimbs is retained in males but falls substantially in females. *Lacerta bedriagae*, *L. laevis*, *L. danfordi* and *L. perspicillata* appear to show some decline in relative rate of limb growth in both sexes, perhaps after a slight initial rise, but the decline is more marked in females. In cases where relative limb length changes with body size, it is important to compare males and females of similar head and body length when assessing sexual differences in limb proportions.

Evolutionary plasticity of limb proportions

It will be seen from Table 1 that hindlimb span often varies substantially among closely related species, for instance within the genus *Mesalina* and within the *Lacerta agilis* group (*L. agilis*, *L. trilineata*, *L. viridis* etc.). This is also sometimes true of forms successively derived from a lineage, such as the genera of the Armatured clade. Such variation suggests that hind limb proportions relative to the body length are quite plastic in evolutionary time, something cor-

roborated by the varying amount of sexual dimorphism and the very different growth patterns encountered. Lineage effects (Arnold, 1994b) in the form of phylogenetic, and specifically developmental, constraint, consequently do not seem to be important in restricting change in relative hind-limb length.

Although there is a clear tendency among species and sexes for increase in relative hind-limb length to be associated with increased difference between fore and hindlimbs, this is also unlikely to represent a strong developmental constraint as the scatter of points in Fig. 3 around the general trend is very substantial. Forms like *Poromera* and *Psammodromus algirus* have similar relative hind limb lengths but differ substantially in forelimb/hindlimb ratios. Conversely *Latastia longicaudata* and *Meroles anchietae* possess a similar forelimb/hindlimb ratio but differ greatly in relative hind limb length. Again, although differences between sexes often follow the general trend between species, there are cases where this is not so.

It is noteworthy that the primitive Palearctic assemblage and more primitive members of the Armatured clade have quite short legs but, given the general plasticity of limb proportions, this seems unlikely to represent a developmental constraint and may simply reflect the habitats they usually occupy. The limb proportions of *Psammodromus algirus*, which belongs to the primitive Palearctic assemblage but often runs on the ground in open areas, as well as climbing, approach those of advanced armatured forms that are nearly all found in such situations.

Functional aspects of differences in limb proportions

Given the plasticity of limb proportions in lacertid lizards and their correlation with kinds of habitats occupied, it would not be surprising if differences between species reflected the functional problems of locomotion in particular environments and were produced by natural selection. A more detailed case for this is given in the rest of this paper but likely advantages of different limb proportions are briefly summarised here. Ground dwelling forms from open habitats get most of their forward thrust when running from the hind limbs. Such thrust is enhanced by greater general hind-limb length relative to the forelimbs, and an extended crus reflected in increased tibial length relative to the femur. The openness of the habitat allows such long hind limbs to be used effectively and probable increase in mass of the caudifemoralis longus muscle increases the power of what is a high-gear system of locomotion that delivers the high speeds necessary to evade predators in situations where cover is sparse.

In contrast, ground dwelling forms that spend considerable time in dense vegetation benefit from generally short limbs which can be deployed in the restricted spaces available. Speeds are lower but concealment from predators is easier. Possibly the greater relative length of the forelimbs reflects greater use in locomotion. Thrust from the small hindlimbs may not be optimal for locomotion and the flexibility of an often relatively long body may reduce its effective transmission. In these circumstances some traction by the forelimbs may be advantageous.

Climbers in vegetation matrixes have similar proportions to those just discussed and are likely to encounter similar locomotory problems. Another factor favouring short limbs in climbers in general is that they give low gearing which is likely to be beneficial when moving upwards against the force of gravity. The relatively long forelimbs in these forms may also allow them to contribute effectively to upward locomotion and they are also important in securing the foreparts, which are above the centre of gravity of the lizard as a whole during vertical climbing and so liable to fall away from the surface being climbed if unattached.

Differences in the caudifemoralis longus muscle

The caudifemoralis longus is the main muscle retracting the femur in lizards and runs from the femoral trochanter posteriorly on to the proximal caudal vertebrae to which it attaches by multiple heads (see e.g. Russell & Bauer, 1992; Arnold, 1994a). The muscle is roughly triangular in shape and its tapering posterior section extends backwards to caudal vertebra 6–13 in lacertids, usually reaching beyond the first autotomy plane discernable in radiographs. The number of autotomic vertebrae to which the caudifemoralis attaches ranges from one to six (L. Hartley, E. N. Arnold, pers. obs). The fact that the muscle extends beyond the first autotomy plane means that some of the most posterior part of the muscle may be lost as a result of caudal autotomy if breakage occurs far proximally, a not uncommon event in some species, for instance *Lacerta vivipara* (Barbadillo *et al.*, 1995). However the effect of such loss on limb function may be relatively small, for the bulk of the muscle lies anterior to the first autotomy plane and the fact that there are attachments to a number of nonautotomic vertebrae means that loss of the posterior section will not result in general loss of function.

There is a phylogenetic regularity in the position of the first caudal autotomy plane discernible in radiographs. In more basal lacertids this is usually on the fourth to seventh caudal vertebra but in most *Nucras* and in its advanced sister group there is a posterior shift and the first plane is usually no further forwards than the eighth vertebra. This shift may mean that the bulk of the caudifemoralis longus is

increased in these lizards and the proportion that remains after proximal autotomy is certainly larger. The number of non-autotomic vertebrae tends to be higher in males than females which means the former may possess a greater bulk of muscle to retract their relatively longer hind legs.

General anatomy of the hind leg (Fig. 5)

In advanced ground dwellers of the Armatured clade, the more distal elements of the hind limb are elongated and it is possible for the leg to be extended until it is more or less straight. The knee is essentially a ginglymus, that is a hinge joint moving mainly in a single plane, but does not run perpendicular to the long axis of the femur instead being angled mesially (Rewcastle, 1980). This results in a complex flexure of the crus on the femur in three dimensions. The mesotarsal joint between the crus and the metatarsal segment of the limb which runs between the astragalo-calcaneum and the other tibial bones, is also primarily a hinge joint and the foot can be extended in line with the crus or flexed until it is more or less parallel with it. However, these hinge joints in the hind leg do not have movement entirely confined to one direction. The crus can twist or swing to a small extent relative to the femur and the foot can flex inwards relative to the crus, some additional motion taking place at the base of the metatarsals. The foot can also twist on the crus to some extent. The hind limb of climbing lizards like *Lacerta oxycephala* is similar, but the distal segments are less elongated and the foot is usually inflected mesially.

Structure of the pes

In this and following descriptions feet are assumed to be placed sole-down on a horizontal surface. The lacertid pes exhibits essentially the primitive lizard structure with no loss or increase of elements in the tarsus, metatarsus or phalanges, the phalangeal formula being 2,3,4,5,4. Digits articulate with the metatarsals via ball and cup joints that allow considerable movement in all directions; in contrast the joints between the distal claw-bearing phalanges and the penultimate ones are double-headed ginglymi that are tightly bound and only permit the claw to move in the vertical plane.

Table 2 Characteristics of the pes in ground dwelling and climbing lacertids (see Figs 7–10).

	Ground dwelling (e.g. <i>Acanthodactylus</i>)	Climbing (e.g. <i>L. oxycephala</i>)
Relative length of metatarsal bones	4 longer than 3	3 longer than 4
Digits 1–4	long	shorter
Relative length of metatarsal + digits 3 and 4	4 markedly longer than 3	4 not much longer than 3
Size of digit 5	short, often minaturised	long
Shape of digits 3–5 in lateral view	gently curved ventrally or straight	clearly kinked
Cross section of digits	rounded	latero-mesially compressed
Shape of phalanges	robust	more slender
Prepenultimate phalanx of digits 2–4 markedly shorter than contiguous ones	no	yes
Claw	long and shallow	short and deep
Articulations within digits	double-headed	simple
Mesial flexibility of digits 1–4	restricted	substantial

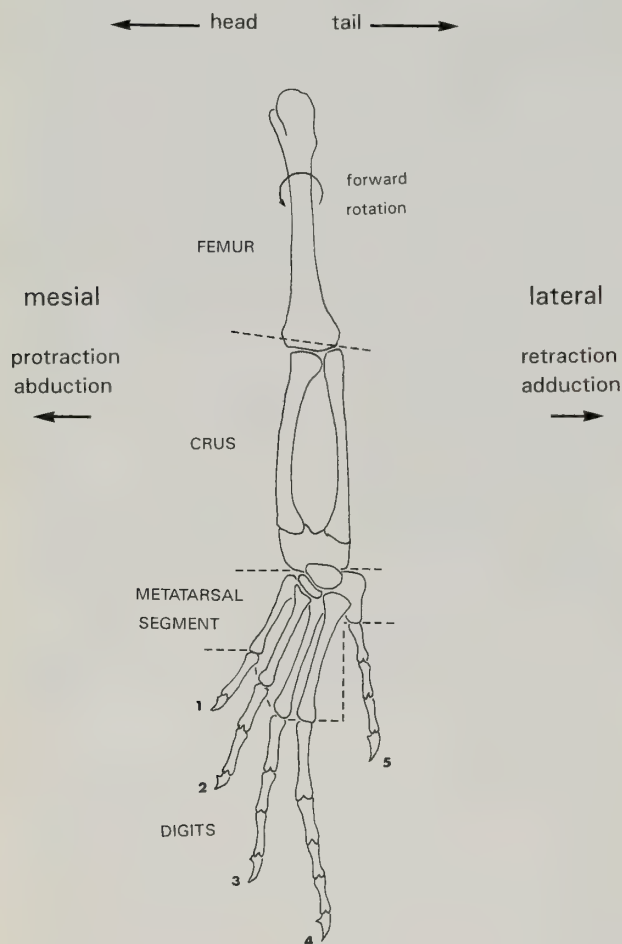


Fig. 5 Skeleton of left hind limb of lacertid from above, showing main elements and regions, orientation and directions of movement.

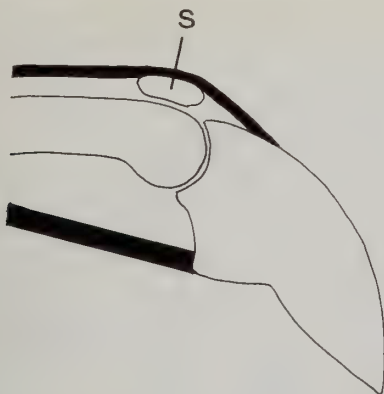


Fig. 6 Lateral view of the bones of the distal part of the digit of a climbing lacertid, showing dorsal and ventral tendons (black) attaching to deep, claw-bearing distal phalanx. The sesamoid bone (s), which can slide on the surface of the penultimate phalanx, displaces the dorsal tendon away from the hinge-line of the articulation between the two phalanges, increasing its moment arm around the centre of rotation and its efficacy in raising the distal phalanx and its claw.

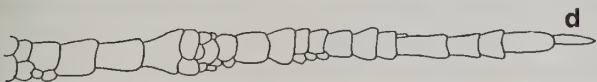
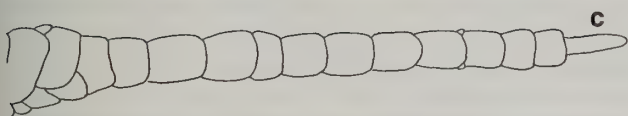
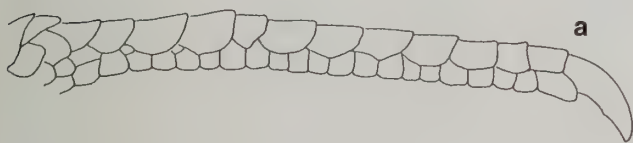


Fig. 7 Lateral and dorsal views of fourth hind digits. a., c. Ground-dwelling lacertid, *Lacerta agilis*. b., d. Specialised climber, *Lacerta oxycephala*.

The dorsal tendon of each digit which inserts on the final claw-bearing phalanx encloses a small sesamoid bone that lies close to the articulation of this phalanx with the penultimate one (Fig. 6). This digital sesamoid acts like a more familiar one, the patella (knee cap) of many mammals, in enhancing the efficacy of the tendon by moving it away from the hinge-line of the articulation and increasing its moment arm around the centre of rotation of the distal phalanx (Curry, 1984).

There are considerable differences in proportions of the pes and in shape and relative orientation of the phalanges and claws. The extremes are found in strictly ground dwelling forms, especially the more advanced members of the Armatured clade, and in those that climb extensively on steep open continuous surfaces. Basic differences are summarised in Table 2.

The pes in ground dwelling lacertids from open situations (Figs 7a,c, 8a, 9a, 10a).

In advanced members of the Armatured clade, like *Acanthodactylus*, the whole foot is large and metatarsal bones 1 to 4, and the digits arising from these, are especially long and increase successively in length. In some instances, such as *Heliobolus lugubris* the metatarsal bones are more or less parallel and bound closely together. Digits 1–4 are also elongated but digit 5, which arises from the highly modified fifth metatarsal bone, is frequently short and may be miniaturised, its phalanges and claw being much smaller than those of other toes. In extreme cases like *Heliobolus lugubris*, the whole fifth toe only extends as far as the distal end of metatarsal 4. Similar substantial reduction also occurs in *Ichnotropis capensis*. Toes are straight or gently curved ventrally when at rest (Fig. 9a) and are rounded in cross section (Fig. 10a). The phalanges themselves are robust (Fig. 9a) and tend to become steadily shorter distally in each digit. Although the prepenultimate phalanx of toes 3 and 4, may sometimes be a little shorter than contiguous ones this is not very marked. The terminal phalanx of each digit and the claw that covers it is relatively long, shallow and curves gently downwards. The prominence on the terminal phalanx, to which the ventral tendon of the digit is attached, is relatively close to the centre of rotation of the claw (Fig. 17c).

Articulations within the digits are double consisting of two horizontally arranged protruberences on the distal end of each phalanx that fit into two hollows on the proximal end of the adjoining one. Although the articulations all appear at first sight to be ginglymi, only the most distal one totally restricts movement to the vertical plane. The others in digits 2–4 allow these toes to be flexed laterally so they can curve quite easily in this direction, even though they are rather stiff basally. However, mesial flexion of these digits is more restricted and they can only form a gentle curve in this direction. The different extents of lateral and of mesial movement within these digits presumably depends on the degree of restriction produced by the ligamentous connections on each side of the articulations and by accessory tendons. Digit 5 swings easily around its base but joints within it, while allowing some movement, are generally stiffer in the horizontal plane than those in digits 2–4. All digits can be flexed extensively downwards and upwards when the muscles controlling them are relaxed.

Similar structure of the pes is found throughout the open-ground forms that constitute the clade made up of *Latastia* and its advanced sister group; it is also approached in many aspects in such ground-dwelling primitive Palaearctic species as *Lacerta agilis* (Fig. 9a, 10a).

The pes in lacertids regularly climbing on steep open surfaces (Figs 7b, d, 8b, 9b–e, 10b).

In *Lacerta oxycephala*, a species that habitually climbs on precipitous rock outcrops (Arnold, 1987), the foot is small and metatarsal

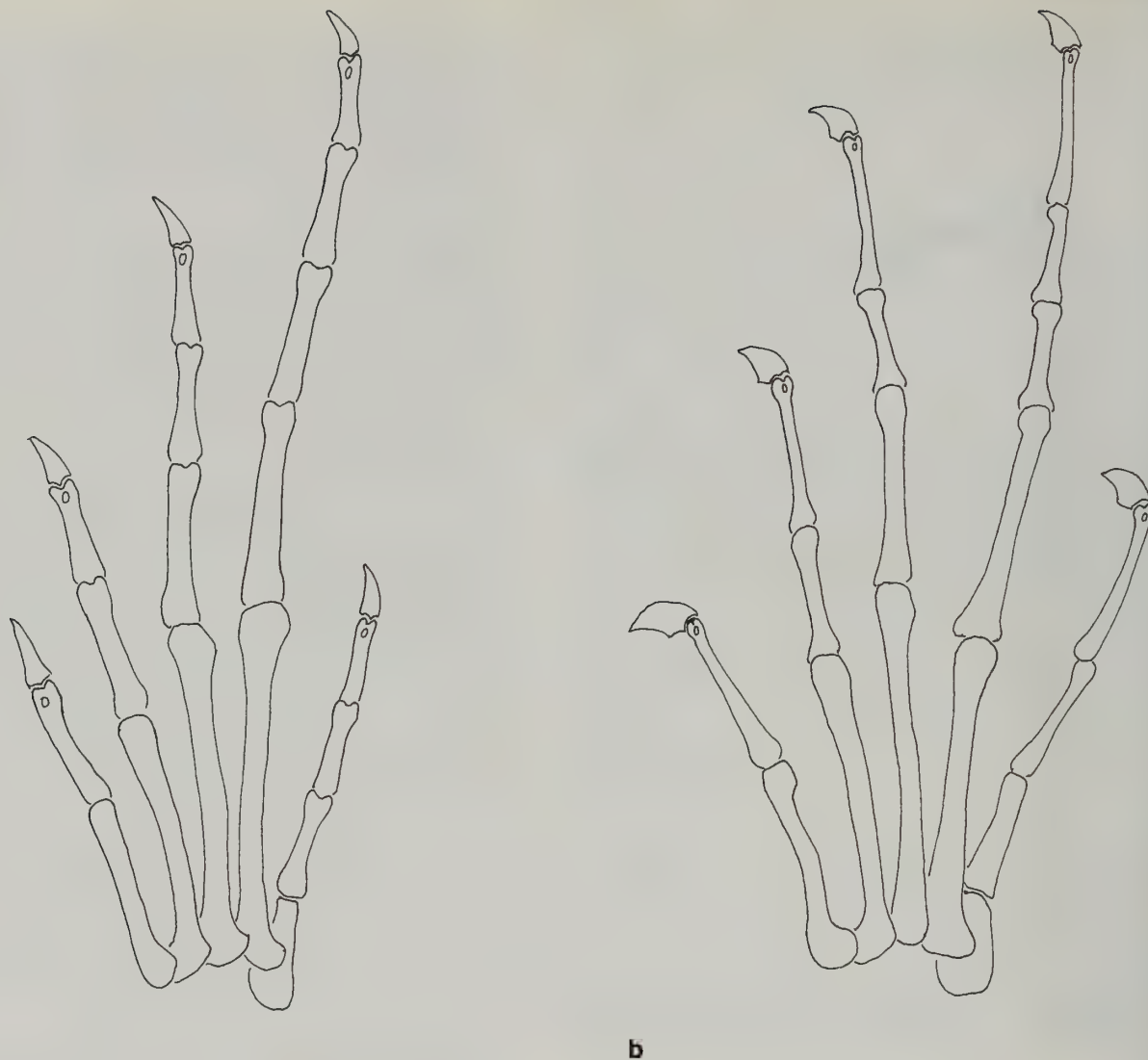


Fig. 8 Dorsal views of right pes of lacertids (digit 1 to left). a. Ground dwelling *Acanthodactylus erythrurus*: metatarsal 4 longest, digit articulations double headed, digit 5 miniaturised. b. Rock climbing *Lacerta oxycephala*: metatarsal 3 longest, digit articulations single, digit 5 large, phalanges slender, intermediate ones in digits 3 and 4 relatively short. For other differences, see Table 2.

bones 1–4, and the digits that arise from them, are quite short. The metatarsals and digits exhibit an increase in length from number 1 to 3 but metatarsal 4 is shorter than metatarsal 3 and, although digits 1–4 increase in length, the shortness of metatarsal 4 results in digit 4 projecting only a comparatively short distance beyond digit 3. Digit 5 is relatively long and unminiaturised, the articulation of its second and third phalanges being about level with the distal end of metatarsal 4. When at rest, digits 3–5 are distinctly kinked in the sagittal plane with abrupt changes of direction along their length (Fig. 9b–d). In digit 3, phalanx 2 is directed downwards, 3 upwards and 4 downwards. In digit 4, phalanx 2 is directed downwards, 3 approaches the horizontal, 4 is flexed upwards and 5 downwards. In digit 5, phalanx 2 is directed upwards, 3 is roughly horizontal and 4 flexed downwards, but there is sometimes marked deviation from this pattern (see p. 77). Kinking when digits are at rest appears to be maintained partly by the form of the envelope of skin that surrounds each digit and that of the ligamentous connexions that surround each interphalangeal joint. If the digit of a live lizard is stretched by

pulling the claw, kinking disappears temporarily, but it is transiently increased if the tension in the tendons lying dorsal and ventral to the phalanges is raised by the action of the muscles that activate them. Kinking is often especially marked in animals preserved in alcohol or formalin because shrinkage of muscle tissue produces similar tension in the tendons.

The digits are mesiolaterally compressed when transversely sectioned through a phalanx (Fig. 10b), instead of having a more rounded profile like ground dwellers. This difference results from the relative thicknesses of the phalanges and the surrounding tendons, especially the ventral ones. In ground dwellers the latter may be considerably more slender than the robust phalanges above them, while in climbers like *Lacerta oxycephala*, where the phalanges are more delicate in build, the stout ventral tendons may be as thick as thicker than these. The penultimate phalanx of each digit is long and gently curved downwards while phalanx 2 in digit 3 and phalanges 2 and 3 in digit 4 are shorter than those proximal and distal to them. The terminal phalanx of each digit and the claw that covers it is short,

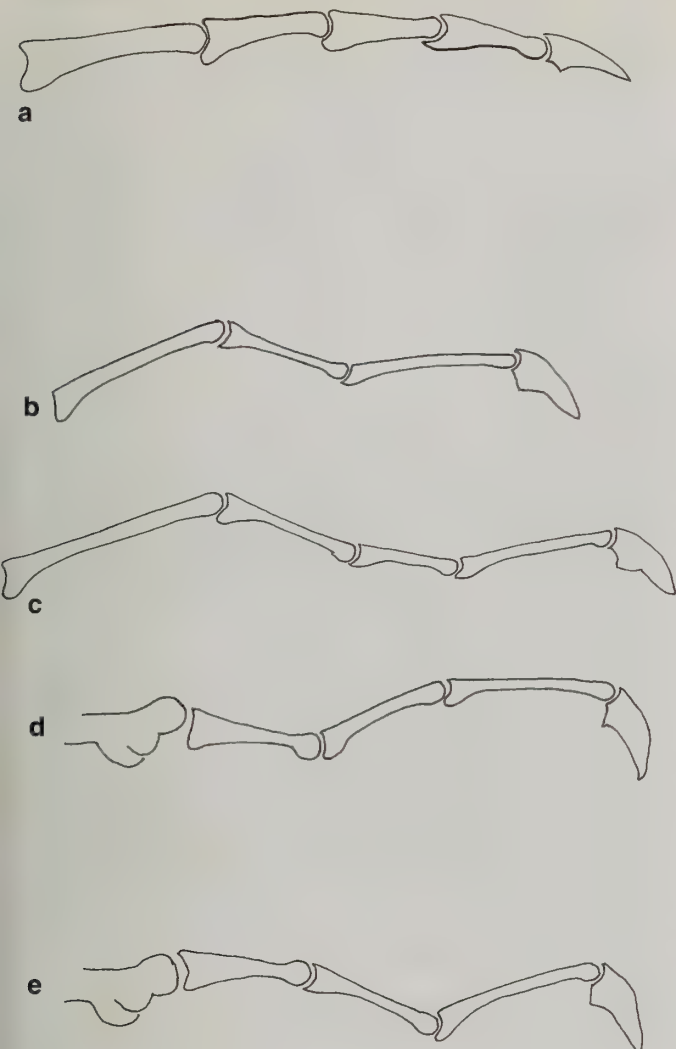


Fig. 9 Digits of pes of lacertids in lateral view. a. Ground dweller, *Lacerta agilis*, digit 4. b–d. Climbing species, *Lacerta oxycephala*, digits 3, 4 and 5. e. Climbing species, *Lacerta perspicillata* showing alternative pattern of flexion in digit 5.

deep and strongly recurved. The prominence on the terminal phalanx, to which the ventral tendon of the digit is attached, is situated well away from the centre of rotation of the claw, conferring considerable mechanical advantage (Fig. 17b). The tendon stands well away from the articulation when the claw is ventriflected; it also tends to do the same under the downflexed joint between phalanges 1 and 2 in digits 3 and 4 (Fig. 17b), and 2 and 3 in digit 5.

Articulations within the digit except for the most distal one are simple, consisting of a single protruberance at the distal end of each phalanx that fits into a cup on the adjoining one. These confer substantial mobility in both the vertical and horizontal planes. As in ground dwellers, digits 2–4 can curve laterally and swing mesially around their base until their proximal phalanges are in line with their metatarsals. Unlike those of ground dwellers, the digits themselves can bend quite abruptly in a mesial direction, as a result especially of flexibility at their penultimate articulations but also, to some extent, of that at the articulations between phalanges 1 and 2 in digits 3 and 4 and that between 2 and 3 in digit 5. Toe 5 is not only lateromesially mobile at its base but also at other joints.

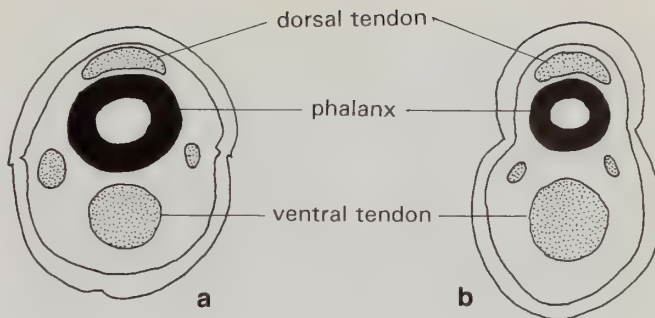


Fig. 10 Diagrammatic transverse sections of toe 4 of a. *Lacerta agilis* and b. *Lacerta oxycephala*, showing differences in relative cross sectional area of phalanx and ventral tendon.

Variations in the direction of kinking in toe 5 of lacertids

Most climbing lacertids possess a pattern of kinking in toe 5 like that found in *Lacerta oxycephala* and described above (Fig. 9d, called here pattern A). However, a minority possess a condition where phalanx 2 is directed downwards, 3 upwards and 4 downwards (Fig. 9e, called here pattern B). Pattern B is found in *Lacerta l. laevis*, *L. l. troodica*, many *L. kulzeri*, *L. chlorogaster*, *L. dugesii* and *L. perspicillata*, *Algyroides*, and the Equatorial African group (Fig. 2) of the Armatured clade; it occurs in weaker form in *Takydromus* and *Poromera*. This variant has consequently evolved perhaps seven times and, at least in Equatorial African group, in *L. chlorogaster* and probably elsewhere, seems likely to have had developed in ancestors that exhibited pattern A. In spite of pattern B originating on several occasions, the details of kinking in toe 5 are often stable across quite large and varied clades, for instance the Equatorial African group. Interestingly, many of the lacertid taxa showing pattern B are known to climb on vegetable structures, such as tree boles and flimsy herbage, which might at first sight suggest that it confers some performance advantage in these specialised situations (but see below)

Patterns of digital kinking in climbers of other families

Many other lizards that climb habitually have kinked digits on the pes and also often on the manus. Attention will be directed here to forms with simple toes, without the complex adhesive pads that occur in many geckoes and anoles. As in the digits of lacertids, the distal part of toes consists of an upwardly directed arc which may contain three phalanges (pattern A) or just two (pattern B).

These patterns occur in various combinations on digits 3, 4 and 5 of the pes and a particular combination for these three toes can be specified simply by a three letter code, for instance for lacertids this would be most usually B.B.A but sometimes B.B.B. There is also some variation in the orientation of the more proximal phalanges of toes 3–5 but this will not be discussed further here. Observed patterns in the distal parts of toes 3–5 in a range of lizards are given below.

A.A.A. *Petrosaurus mearnsi* (Phrynosomatidae); *Plica plica* (Tropiduridae); *Gonocephalus modestus*#, *Draco blanfordii* (Agamidae); *Agamura persica*, *Cyrtodactylus consobrinus* (Gekkonidae); *Xantusia henshawi*, *Lepidophyma flavimaculata* (Xantusiidae); *Platysaurus*, *Pseudocordylus* (Cordylidae); *Mabuya quinquetaeniata* (Scincidae).

A.B.A *Tropidurus torquatus* (Tropiduridae).

B.B.A *Agama caudospinosa* (Agamidae), most lacertids.

B.B.B. *Varanus indicus*#, *V. mitchelli*#, *V. tristis* (Varanidae); *Cryptoblepharus boutoni* (Scincidae); several lacertids#.

B.A.B. *Cnemaspis africanus* (Gekkonidae).

When three toes are considered, there are eight possible combinations of the two patterns of kinking. BBB* (3), BBA* (2), BAB* (1), BAA, ABB, ABA* (1), AAB, AAA* (9). Five of these (asterisked) have already been observed in the small sample of climbing lizards examined; figures in parentheses indicate the number of cases encountered of each.

As already noted, pattern B in toe 5 is most usual among lacertids in forms that climb on vegetable structures (marked#), but when members of other families are also considered it is clear there are species with fifth toes exhibiting pattern A in this situation. Overall, there is no obvious correlation of pattern B with climbing on vegetable structures in any of toes 3–5.

The widespread occurrence of toe kinking in climbing lizards and its repeated evolution suggests that it confers performance advantage in this locomotory situation. However, the variety of patterns, including differences in the more proximal parts of toes 3–5, and the fact that they occur in various combinations in these toes, suggests that the exact arrangement of phalanges may be rather arbitrary in functional terms. Nonetheless, the existence of a particular pattern across some clades within the Lacertidae indicates that, once a pattern for a toe has become established, it may persist for long periods, even though multiple shift from pattern A to pattern B in toe 5 has also occurred. If the pattern of kinking is more or less arbitrary in functional terms, shift from one to the other might sometimes occur after an intervening non-climbing phase when the initial pattern was lost, but there is no overt evidence for such interludes.

The structure of the manus

As with the pes, the lacertid manus always possesses the primitive lizard phalangeal formula, which in this case is 2,3,4,5,3. The manus is also like the pes in the way the digits articulate with the metacarpals via ball and cup joints and in having terminal articulations that are tightly bound gynglymi with associated sesamoid bones. Metacarpal 3 is always the longest and numbers 1 and 5 the shortest, the digits are more equal in length than those of the pes and are capable of being broadly spread.

The manus in ground dwelling lacertids from open situations (Fig. 11a, Table 3)

In advanced members of the Armatured clade, the manus is often quite small compared with the pes although this differential is less obvious in species from soft-sand habitats. The longest digit is usually number 3 or this is subequal to 4. Toes are straight or gently curved ventrally and are rounded in cross section. The phalanges are often very robust, frequently more so than in the pes, and except for the terminal ones, tend to be subequal within a digit. The relative brevity of toe 4, which has most phalanges, means that these are particularly short. The final phalanx of each digit and the claw that covers it tends to be long, shallow and curves gently downwards. Articulations within digits are double and, as in the pes, mesial flexion of the toes is restricted.

The manus in lacertids regularly climbing on steep open surfaces (Figs 11b,c, Table 3)

In forms like *Lacerta oxycephala*, the manus is smaller than the pes but comparatively much larger than in many ground dwellers. The longest digit is usually number 4 and digits are lateromesially compressed; numbers 3 and 4 are flexed downwards at the articulation of phalanges 1 and 2, and somewhat upwards at the penultimate articulation, as in the other digits. Phalanges are slender, the penultimate ones being relatively long and slightly curved downwards; phalanx number 2 of digits 3 and 4 and also number 3 of the latter are

Table 3 Characteristics of the manus in ground dwelling and climbing lacertids (see Fig. 11). Differences in transverse section of the digits, shape of phalanges, claws and articulations within digits are similar to those in the pes.

	Ground (e.g. <i>Acanthodactylus</i>)	Climbing (<i>L. oxycephala</i>)
Longest digit	3, or 3 and 4 subequal	4
Phalanx 2 of digits 3 and 4 and phalanx 3 of digit 4 shortened	weakly	strongly
Phalanx 2 of toes 3 and 4 flexed downwards	no	yes
Digits can be very widely spread	no	yes
Mesial flexibility of digits	restricted	substantial

shorter than the ones bordering them. The final phalanx of each digit and the claw that covers it is short deep and recurved. As in the pes, the main ventral tendons are offset in the regions where digits are flexed downwards. Articulations within the digits are simple involving a single cup and ball arrangement and the digits can be abruptly flexed in the horizontal plane both mesially and laterally, especially in the area of the penultimate articulation.

The manus of *Holaspis guentheri* (Fig. 11c) deviates considerably from that characteristic of other lacertids climbing on continuous open surfaces. Digits 2–5 are more subequal in length, and numbers 3 and 4 are conjoined for the length of their first phalanx, penultimate phalanges are extremely long and more curved ventrally than in other lacertids and phalanx 2 of toe 3 and phalanges 2 and 3 of toe 4 are very short and flexed downwards. This degree of distinctiveness in the manus of *Holaspis* contrasts with that of the pes which, although it has the features usually associated with climbing on open surfaces better developed than in *Lacerta oxycephala*, does not differ radically from this species in its general form.

Characteristics of the feet in other lacertids

The numerous primitive Palearctic lacertids and more basal members of the Armatured clade that climb to a significant extent on open surfaces have at least less marked versions of the foot characters that form a syndrome in a specialised climber like *L. oxycephala*, although the foot tends to be longer. Thus, the claws are relatively deep, the toes compressed and kinked, and metatarsal 3 is longer than 4 in the pes. These features occur, for instance, in many 'archaeolacertas', some *Podarcis* such as *P. hispanica*, *Algyroides nigropunctatus* and *A. marchi*, members of the *Lacerta agilis* group but not *L. agilis* itself, *Gallotia*, *Psammmodromus algirus*, *Australolacerta* and most members of the Equatorial African group. Independent shifts to the more marked version of the syndrome are found in such frequent climbers as *Lacerta perspicillata*, *Omanosaura* and especially *Holaspis*.

Forms that climb in vegetation matrixes, like *Gastropholis*, some *Takydromus* and *Poromera*, tend to have relatively weak versions of the climbing pattern but may also possess distinctive features for instance, in the latter two genera, separation between the digits may extend proximally between the distal parts of the metacarpals and metatarsals, allowing wider spread of the digits.

The manus and pes features that characterise advanced ground-dwelling members of the Armatured clade have developed in other ground-dwelling lacertids, at least in restricted form. Thus metatarsal 4 is about equal to number 3 in *Lacerta agilis*, *Psammmodromus hispanicus* and *Adolfus alleni* and is longer in some *Podarcis* that run extensively on the ground, such as *P. sicula* and *P. taurica*. Digit 5 of

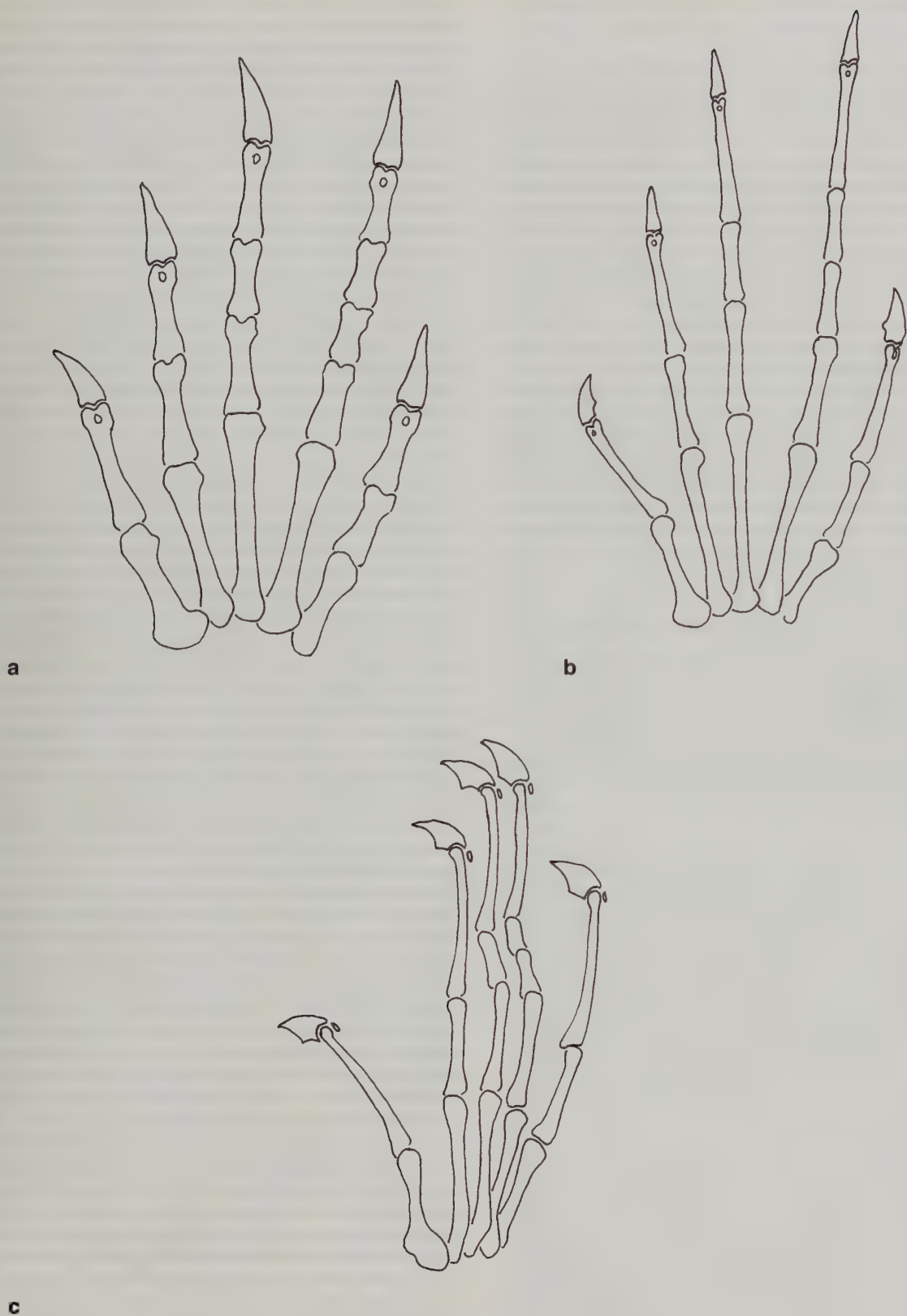


Fig. 11 Right manus of lacertids (digit 1 to left), a., b. dorsal, c. anterodorsal. a. Ground dwelling *Acanthodactylus erythrurus*: digit 3 longest, phalanges robust. b. Rock climbing *Lacerta oxycephala*: digit 4 longest, phalanges slender. c. *Holaspis guentheri*: toe 5 long, toes 3 and 4 strongly kinked. See Table 2 for other differences between a. and b.

the pes may be small in some of these forms and the digits are often not strongly kinked and have robust subequal phalanges and rounded cross sections. The syndrome is best developed as whole in *Psammodromus hispanicus* and *L. agilis*.

In some cases, a mixture of features typical of ground-dwelling and other activities occur. This may be a result of functional compromises, for instance in forms that are substantially ground dwelling but also occur in other situations. In *Lacerta vivipara*, a ground form that spends substantial time in dense grassy vegetation, many features associated with ground dwelling are present but metatarsal 4 is short and toe 5 quite long. Possibly the way the feet of this species are used in traversing vegetation has similarities to climbing. In *Poromera*, the foot has some features associated with ground locomotion and some with climbing quite strongly developed. However, in spite of probably sometimes climbing in vegetation, the hands and feet of *Philochortus* are essentially of the ground type.

Overall, direction of change in foot morphology appears to follow closely that of structural niche in lacertids (p. 00).

The variations in the pes found in lacertids are paralleled quite closely in some other families. For instance, within the sister group of lacertids, the Teiioidea, the Teiidae which are mainly ground dwelling in open situations have the pedal characteristics of lacertids occupying similar structural habitats. As here, the fifth toe is usually miniaturised and in *Teius* disappears entirely, something that also occurs in the ground running agamid *Sitana* (Russell and Rewcastle, 1979).

Special structures of the digits

In primitive Palaearctic lacertids and more basal members of the Armatured clade including *Nucras*, the toes are covered above with a single row of unkeeled scales along their length and below by a row of scales or lamellae that correspond more or less to those above. The lower row is often tubercular and each scale may be divided centrally, although this feature varies considerably, sometimes even among subdigital scales on the same toe. A number of modifications of this primitive external toe structure occur.

Expanded subdigital lamellae

Takydromus kuehnei is unique among lacertids in having the more proximal subdigital lamellae of the digits clearly expanded laterally to form a narrow pad superficially similar to those of geckoes such as *Cyrtodactylus*. This feature, towards which there is a slight tendency in some other *Takydromus*, may possibly enhance adhesion on the surfaces of the vegetation, among which these lizards are often found, by increasing the lower surface of the toes. However, SEM studies reveal no microornamentation of adhesive setae on the subdigital lamellae of *Takydromus kuehnei* (pers. obs.), such as are found in other pad bearing climbing forms including many geckoes and anoles, and the skink, *Prasinohaema virens* (Williams & Peterson, 1982).

Keeling of subdigital scales

Instead of being tubercular, the scales beneath the digits of lacertids may bear keels which, in ventral view, appear more or less parallel to the axis of the digit. In these cases the free edge of each scale and its keels are directed obliquely downwards, the latter ending in projections. When a toe is put down on a smooth flat surface, contact with this is largely limited to these points. Downwardly directed scales with keels ending in projections also occur on the palms and soles.

A tendency to keeling, often with considerable individual variation occurs in most *Psammodromus* species and in *Philochortus*.

Fully developed and consistent keeling is found in the advanced clade of ground dwellers in the Armatured clade that constitutes the sister group of *Philochortus*. Full keeling has evolved independently in *Psammodromus hispanicus* (presumably from the intermediate condition in other members of the genus), in *Omanosaura cyanura*, and in *Lacerta cappadocica*; there are thus four origins of the condition within the Lacertidae.

The number of keels on subdigital lamellae varies: two is most frequent but there are sometimes several, something which is commoner on the manus than the pes. Single keels also occur, in *Lacerta cappadocica* and in dune dwelling species of *Meroles*, *Acanthodactylus* and *Eremias* in which they are associated with less downward projection of the edge of the scale and little development of projections at the tips of the keels. In at least the first two genera, the shift to single keels has happened more than once.

Keeling on subdigital scales may vary within a species, for example there may be one to several in different populations of *Acanthodactylus grandis* (Arnold, 1983). This suggests keeling is quite labile in detailed form. Species that live exclusively on very fine aeolian sand may lose keeling secondarily, something that has developed independently in *Meroles anchietae* and *Eremias* (*Scapeira*).

Evolutionary shift to keeling does not appear to be related to changed locomotory requirements and instead may be more important in protecting the toes from high temperatures (Arnold, 1973). Some desert lacertids are at least briefly active on surfaces as hot as 60°C (pers. obs.), even though their digits incorporate delicate blood vessels and nerves. In this situation, limiting contact with the ground largely to the projections at the end of keels is likely to reduce heat intake, especially as keratin, of which the subdigital lamellae are formed, is a good insulator. If this is so, keeling may not be important as such but only as a means of providing support for the projections that actually contact the ground. Similar support of projections by keels is found in the belly scales of many *Takydromus* species, although here the projections appear more important in increasing frictional contact rather than in insulation (Arnold, 1997).

In the Armatured clade, the shift to keeling is associated with movement into hot open ground habitats and the same is true in *Psammodromus*. The *Lacerta* and *Omanosaura* with keeled digits are rock-dwellers but in particularly warm areas.

It is not clear why aeolian sand species often exhibit reduction from double or multiple to single keels with less downward flexion of the free edges of the subdigital scales, and sometimes totally lose these features. One possibility is that the keeling and the associated projections will not be able to keep the digits substantially out of contact with the ground, because the toes of running lizards usually sink into soft sand, at least to some extent, so projections supported by keels will not restrict contact. In fact, the sinking may also reduce the problem of heat load since the digits are only briefly in contact with the very hot uppermost layer of sand and pass rapidly through it into the rather cooler layers below.

Outside the Lacertidae, digital keeling occurs in many other lizard families and is usually associated with hot substrata. It is found in many iguanians, scincids and cordylids that occur in sunny situations, but is absent in largely nocturnal or mesic clades such as gekkotans, xantusiids and anguids. The development of full keeling is probably associated with modest body size, a situation in which the problems of overheating of the extremities are likely to be particularly acute.

Digital fringes

Lateral and often mesial fringes of pointed scales on the digits have developed in at least five separate clades of the Lacertidae: in

Acanthodactylus, *Meroles*, *Eremias*, *Holaspis* and, in restricted form, in *Pseuderemias*. In *Acanthodactylus* a lateral scale row is present on the digits of manus and pes of all species, but an additional mesial row has developed on the manus perhaps three or more times in groups living mainly on soft sand (Arnold, 1983; Harris, Arnold & Thomas, submitted b). *Meroles* is similar in that all species have a lateral scale row on all digits, and a mesial row on those of the manus in a clade found on soft sand, consisting of the subgenus *Saurites* and *Meroles anchietae*. A mesial row occurs on the pes as well in *Meroles anchietae* which is found in the most extreme of such habitats (Arnold, 1991). Lateral and mesial scale rows have also evolved on all feet in the aeolian sand species of *Eremias* (*Scapteira*). *Holaspis* is distinctive in exhibiting additional scale rows only on some of the digits of the pes: digits 3 and 4 possess lateral and mesial rows, while digit 5 has a lateral row which is continuous with similar scales on the trailing edge of the hind leg and the sides of the tail.

In sand dwelling forms, the additional scale rows on the digits, which are often elongated and projecting, act rather like snow shoes during locomotion, reducing the tendency of the feet to sink into the yielding substratum (Carothers, 1986; Luke, 1986) and thus increasing effective thrust when running. However, it is notable that, although ground dwelling lizards obtain most locomotory thrust from the hind legs (p. 000), additional mesial rows of scales develop first on the manus. This may be because the forefeet especially are used in digging for food and to construct burrows and in this situation the fringes increase the efficacy of digging by broadening the toes so they shift more sand. Possibly, where sand is not especially soft, the functional advantage of an additional scale row is more critical in digging than running.

Although lateral expansion of the digits appears to confer advantage when running and digging in soft sand situations, it is less clear why expansion should be achieved by separate additional scale rows in lacertids, since some sand-dwelling lizards in other families merely have the usual dorsal and ventral scale rows on the digits extended horizontally to form fringes (Luke, 1986). Indeed in sand lacertids without a mesial row, the dorsal scale row may project in this way. Possibly, separate rows of scales on the sides of the digits do not actually give better function, in impeding the toes when they are pressed into the substratum, than fringes produced from dorsal and ventral rows. They may however be advantageous in environments where sand is very soft because fringes made up of independent scale rows can flex more easily ventrally, reducing impedance when digits are withdrawn from the sand.

In contrast to their function in sand dwellers, the additional digital scale rows of *Holaspis* probably provide extra lift when this unique lacertid glides through the air (Arnold, 1989b). In some iguanians such fringes permit the lizards to run across the surface of water (Luke, 1986). Although fringes made up of additional scale rows on the digits thus occur in three superficially quite different situations, in all of them they slow or prevent passage of the feet through fluids.

Not only have digital fringes in lacertids been elaborated by subsequent addition of separate lateral scale rows, but the length of the scales forming these also varies, often showing considerable correlation within a genus with the softness of the substratum usually occupied (Arnold, 1983). However, although some members of primarily sand dwelling clades appear to have reverted to firmer substrata, for instance *Meroles suborbitalis*, there are no certain cases where additional digital scale rows have been subsequently lost even though their degree of projection may be reduced.

LOCOMOTION AND FUNCTION

Some aspects of locomotion in habitual open ground lizards and in climbers are contrasted in Table 4

Locomotion in ground dwellers of the Armatured clade (Figs 12–13)

The following observations are based on *Heliobolus lugubris*, *Meroles cuneirostris*, *M. reticulatus*, *M. anchietae*, *Eremias arguta*, *Acanthodactylus boskianus* and *A. pardalis*. These were either videoed dorsally and laterally at 25 fields/sec and an exposure of 1/1000 sec., or filmed at 16–48 frames/sec. *Meroles cuneirostris* was also videoed at 200 fields/sec. Most runs were conducted on a flat cork surface but animals were also allowed to sprint across soft sand and the footprints produced used to check stride length and relative thrust of the fore and hind feet, as indicated by pressure waves in the sand produced at the trailing edge of the prints.

Lacertid lizards use all four legs when running. The gait is sprawling, that is the humeri and femora project from the body roughly in the horizontal plane, and the steps of individual limbs can be divided into two phases: the power stroke when the limb is retracted and actually delivers thrust, and the recovery stroke when it is brought rapidly forwards in preparation for the next step. Typically the fore and hind limbs work in diagonal pairs, for instance, the right foreleg and left hindleg are brought forwards in the recovery stroke at about the same time and are retracted more or less together in the power stroke; there may however be a slight lag, so that a hindlimb starts to move forwards after the contralateral forelimb.

At extreme phases of the locomotory cycle, the forelimb on one side of the body is directed backwards and the hindlimb forwards, so they approach each other or overlap, while on the other side of the body the limbs are directed diametrically away from each other. In general, strictly ground-dwelling lizards of the Armatured clade carry the body well away from the substratum when running. At the end of the power stroke of a hind limb, the lizard may be balanced on the toes of a single foot and this is followed by a gliding phase when the animal ‘floats’ forwards with all limbs off the ground.

Because of this floating phase, the total stride of each limb pair, that is distance between ground contact of left and right feet, may be substantially greater than the anatomical stride which is the distance between the feet of a limb pair when they are maximally spread forwards and backwards. As forelimb span is much less than hindlimb span in ground dwellers, the difference between total and anatomical strides is much greater for the forelimbs and they are both off the ground for much longer periods than the hindlimbs.

The posterior body flexes laterally to some extent during rapid locomotion towards the side on which the hindlimb is moving

Table 4 Some characteristics of open ground and climbing locomotion in lacertids specialised to these activities.

	Fast ground	Vertical
Body close to substratum	no	yes
Anatomical stride of forelimbs	short	long
Hind leg delay	some	more
Crus extended right forwards	yes	no
Hind step length/snout-vent distance	often >21	often < 1
Floating phase	yes	no
3 legs often in contact	not usually	yes
Toe 5 makes positive grip	no	often
Rise on toe tips at end of stride	yes	no

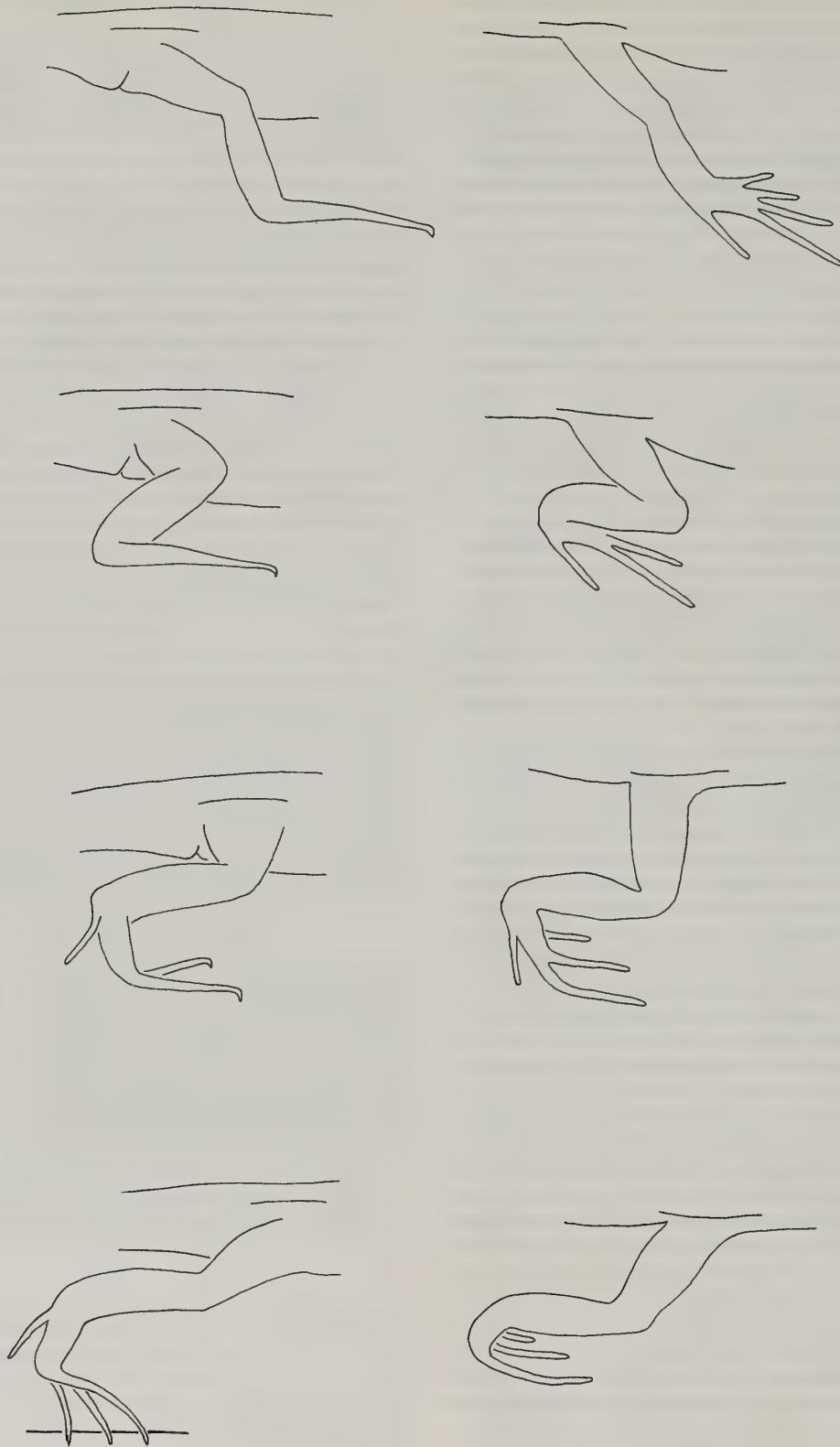


Fig. 12 Movements of hind leg of ground dwelling lacertid when running (left – lateral views, right – dorsal views). a. Beginning of power stroke: limb extended anterolaterally with toes 1–4 directed forwards and spread with claws inserted in substratum. b. Crus flexes on femur. c. Femur begins to retract, crus becomes more horizontal as femur rotates forwards and the metatarsal segment rises and is turned laterally bending the toes. d. Femur continues to retract, crus and metatarsal segment extends backwards and lizard rises on tips of toes 2–4.

forwards. This increases the length of the hind limb step which in the more long-legged species may be substantially longer than the body. Wild *Meriones anchietae* about 60mm from snout to vent had step lengths of 80–150mm (measured from tracks at Gobabeb, Central Namibia in April, 1994). As might be expected from the greater relative lengths of time they are in contact with the ground, hind limbs are far more important in fast ground locomotion than forelimbs. That they deliver more thrust can be seen from tracks in sand where hind limbs produce footprints with a strong posterior pressure wave caused by their powerful backward extension, whereas forelimbs tend to produce simple shallow pocks, indicating that their main role is to provide intermittent support to the foreparts.

Movements of the hind limb (Fig. 12)

When animals are running fast, the hind leg is brought forwards so that it is extended in generally anterolateral direction with the main axis of the metatarsal segment often lying approximately parasagittally or somewhat anterolaterally and digits 1–4 directed forwards and spread (Fig. 12a). The femur lies roughly in the horizontal plane, while the crus is directed obliquely downwards and the foot is placed flat on the ground with the claws of toes 1–4 flexed downwards and inserted into the substratum. Toe 5 often projects more laterally.

In the first phase of the power stroke, the crus flexes on the femur (Fig. 12b). This results in the femur moving forwards but, as the line of flexion of the knee is offset mesially, its distal extremity passes over the crus which changes orientation so that, from being directed anterolaterally, the crus swings until it is directed ventroposteriorly in a parasagittal plane.

At this stage, the femur begins to be retracted, its distal end descends somewhat and it also rotates forwards (when viewed from above) about its long axis (Fig. 12c). The crus also again becomes less flexed relative to the femur and these various movements change its orientation, so that it becomes more or less horizontal but still lies in a parasagittal plane. As this occurs, the metatarsal segment rises proximally, beginning with its lateral edge, so that it is now directed downwards and outwards. In firm substrata, the claws maintain their position so that this reorientation of the metatarsus then results in some mesial bending of the toes in the horizontal plane to accommodate it; however flexing is limited by the stiffness of the toes in this direction.

The femur continues to be retracted until it is directed anteroposteriorly (12d). At the same time the crus unflexes further so that it maintains its parasagittal orientation. By now, the metatarsal segment is completely lifted from the ground and this raises the base of the toes which, as well as being bent mesially, become flexed downwards and the lizard rises on to the tips of toes 1–4 and then just 2–4 so that, at this stage, it is hyperdigitigrade. Final thrust in the step is thus delivered entirely through the claws which act like the spikes on an athlete's running shoes. During this phase the whole leg extends and the upper surface of the metatarsal segment may even be directed anteroventally.

During a step, the lizard thus uses extension of all parts of the hindleg to provide thrust: femur, crus, metatarsals and digits. After this the muscles controlling the ventral tendons of toes 2–4 may relax so these digits dorsiflex and the claws are pulled free. Toe 5 plays very little part in fast locomotion in specialised ground dwellers and leaves the ground at an early stage.

In the rapid recovery stroke, where the hind limb is brought forwards before the next step, it is raised high, partly flexed and then extended forwards. During this process, the femur is protracted and its forward rotation is maintained, so that forward flexion and

extension of the leg takes place more or less in the horizontal plane and the foot is oriented with its mesial edge downwards. This allows the distal portions of the limb to be kept well clear of the ground, so that it is less likely to be impeded by any irregularities in the substratum or by projecting plants. It also means that when the foot does make contact with the substratum at the beginning of the power stroke, it may still be orientated with its mesial edge downwards, although it is then immediately placed flat on the ground as a result of backward rotation of the femur. If the toes do encounter an object that hinders their forward motion during the recovery stroke, the fact that the upper surface of the foot is directed forwards means that they can simply be passively ventriflexted and brushed aside, so the leg can still progress anteriorly. The toes are also capable of passive lateral movement around their joints with the metatarsals, especially when the foot is in the process of being placed sole-downwards on the ground.

There is some variation in fast hind leg motion in armatured ground-dwellers, which may partly result from the nature of the substratum and its irregularities. Thus the foot may be clearly directed anterolaterally at the beginning of the power stroke and the claws may slip in loose soils so that the foot tends to rotate outwards more at the end of a step. Some species also have characteristic features during fast ground locomotion; for instance, in *Acanthodactylus boskianus* the foreparts are carried particularly high.

Rotation of the femur and supposed restrictions on its movement

Rotation of the femur about its long axis is a very significant feature of hind leg movement during locomotion (Rewcastle, 1983). It enables the path of extension of the crus during the power stroke to be different from that of its flexion, allows the leg to be brought forwards orientated more or less in the horizontal plane well above the ground, and explains why the foot may be initially put down mesial edge first.

It has sometimes been assumed that the femur in lizards cannot be adducted far posteriorly because its trochanter was believed to jam against the ventral rim of the acetabulum (Rewcastle, 1983). However, in all the lacertids studied, substantial posterior adduction is regularly observed and no restriction of the kind envisaged is observable in skeletal material.

The supposed problem of crural rotation

There has been considerable discussion of a supposed problem of rotation within the distal hind limb (see for instance Rewcastle, 1983). If the foot is assumed to maintain its position during the power stroke, while the angle of the femur in the horizontal plane changes relative to it during adduction, there would have to be a rotational twist within the intervening crural area, to accommodate the change in relative position of these elements. The screw-like nature of the mesotarsal joint between the crus and foot actually permits some twisting (Rewcastle, 1980) and various other factors reduce the amount that is actually required: 1) The angle of the knee joint allows the crus to swing, from being in line with the femur at the beginning of the power stroke to being directed backwards, without disturbing the foot; 2) forward rotation of the femur and descent of its distal extremity also helps minimise twisting of the lower limb; this is also true of 3) reorientation of the metatarsal segment, 4) bending of the toes, and 5) the general mobility of the tarsal area. These factors, involving changes in orientation of the distal femur and of the proximal foot preclude any substantial problem of crural rotation.

A partial model of hind limb movement

The movements of the hind leg of lizards during locomotion take

place in three dimensions and are not always easy to envisage from a written description and diagrams. However a clearer idea of some of the main aspects can be obtained by making a simple model out of a strip of card with folds inserted to represent articulations between the main elements (Fig. 13). The model can be used to demonstrate the pattern of flexion between the femur and crus, the subsequent reorientation of the latter element in the parasagittal plane and associated lifting of the metatarsal segment brought about by partial retraction and rotation of the femur, the benefits of femoral rotation in allowing the limb to be partially retracted and extended in the horizontal plane as it is brought forwards in the recovery stroke, and the restricted nature of the problem of rotation in the crural region. It should however be born in mind that there is more play in the actual joints than the model indicates. Such a model is also useful in appreciating the rather different motions of the hind leg in climbing species.

Other hind limb gaits in ground-dwelling lizards – continuous gearing

Although lizards are often stated to have only a single gait, in contrast to many mammals, the hind limbs are used in a range of ways that are largely correlated with speed. Stationary lacertids may commence movement by thrusting with both hind legs, especially if startled, so accelerating before a step pattern is established. In slow walking, the excursion of the femur may be restricted and, instead of being brought forwards, the crus may be kept largely flexed, so that it is never directed forwards and the soles of the feet may be orientated rather laterally, a result of forward rotation of the femur.

At increasing speeds, femoral excursion is greater and the crus may be brought forwards until it is roughly perpendicular to the body with the foot directed anteroposteriorly. Finally, the crus is extended fully forwards and the femur rotated backwards at the beginning of the power stroke, as described above. These substantial changes in the way the hindlegs are used act like continuously variable gears. As might be expected, the body is held closer to the ground in the slower gaits as forward rotation of the femur during these permits a more lateral use of the whole limb.

Movements of the foreleg in ground-dwellers

At the beginning of the power stroke, the humerus is directed anterolaterally and the lower limb and digits point forwards. During retraction the forelimb turns over until its underside is uppermost. At first the manus is placed palm-down, but the lizard rises on the distal toes as the lower limb becomes more or less vertical. However, the toes usually dorsiflex at the end of the stride. As with the hind leg, the foreleg is raised high when it is brought forwards in the recovery stroke.

Functional aspects of the limbs and feet of ground-dwelling lacertids

It is now possible to assess the functional importance of limb morphology in ground dwelling lacertids. The long legs, in which the more distal elements – crus, metatarsal segment and digits – are differentially elongated, are responsible for the extended stride of these species, and the way the metatarsal bones are bound closely together in some forms increases the rigidity of the metatarsal

segment. The way the main adductor muscles, especially the caudifemoralis, are attached proximally to the femur confers high mechanical advantage on the locomotory system, which in this respect and the elongation of its distal elements parallels those of other fast amniote runners such as horses.

The regular downward curve of the toes, maintained by joint capsules and tension in the dorsal and especially ventral tendons at the end of the stride, and the restriction on medial flexion, ensure that thrust is delivered to the ground efficiently. The robust phalanges with joints of restricted flexibility are clearly suitable for resisting the compressive and shearing forces produced at this time, when the lizard may sometimes be balanced on the tips of very few toes. Steady increase in length from the first toe and its metatarsal to the fourth means that the claws of these digits can be well-spaced when inserted in the ground, ensuring a wide area of contact with the substratum so a good grip is more likely, even on shifting surfaces; the generally large size of the foot also contributes to this spread and the long lightly curved claws are more likely to gain effective purchase in earth or sand than short recurved ones. Reduction of the fifth toe is comprehensible in as much as it is virtually unused in fast locomotion.

The very robust phalanges of the manus may not be specifically associated with locomotion but could be important in digging, something advanced ground lacertids accomplish largely (or entirely in the case of *Heliobolus lugubris*, personal observations) with their forelegs. Possibly the relatively large manus of soft-sand dwellers is also functionally associated with digging.

Ground locomotion in climbing species

Lizards that habitually climb, like *Lacerta oxycephala*, *L. perspicillata* and to a lesser extent, *L. nairensis*, run quite efficiently on the ground and often extend the crus fully forwards. However, they tend to carry the body less high than specialised ground-dwellers, partly because their limbs are generally shorter and the crus especially so, and these features also limit stride length. Habitual climbers do not rise on to the tips of their toes at the end of the stride and, instead of the digits flexing downwards, they flex dorsally, toes 2–4 bending at the penultimate articulation between the phalanges, so the pes rotates over the inserted claws (Fig. 17b). This shortens effective stride length still further. Climbing species also tend to keep the hind limb closer to the substratum during the recovery stroke.

The distinctive features of ground locomotion in habitually climbing forms all have functional advantages during climbing (p. 000). A similar but more extensive carry over of features advantageous in climbing to horizontal locomotion occurs in the gecko, *Gekko gecko* (Zaaf, Aerts *et al.*, 1997).

Locomotion in climbers on steep open surfaces (Figs 13–17)

Most detailed observations were made of *Lacerta oxycephala*, which was filmed dorsally and laterally when climbing on a near vertical rock slab. *L. perspicillata*, *Algyroides nigropunctatus* and *A. marchi* were also examined by film or video; in most cases, speeds and exposures were the same as for many ground dwelling lizards but *Algyroides nigropunctatus* was also videoed at 200 fields/sec.

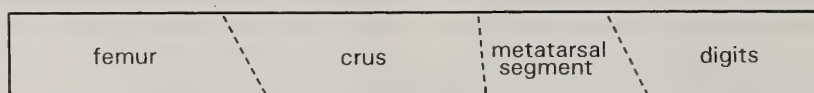


Fig. 13 Simple model of right hind limb of lacertid. A strip of card cut and folded as indicated by broken lines can be used to demonstrate the main movements of the hind leg elements in a running lizard.

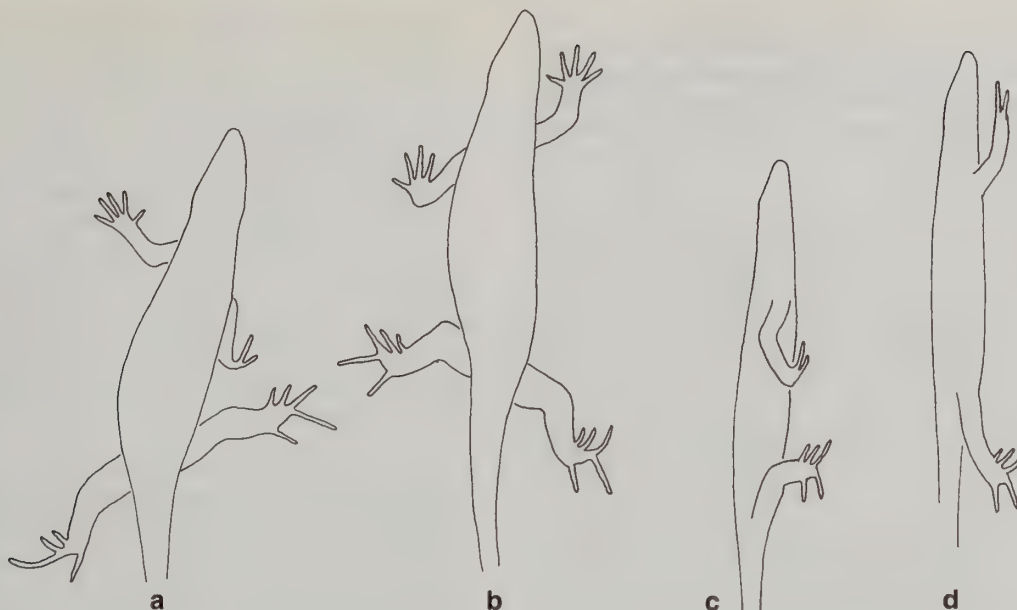


Fig. 14 Views of specialised climbing lacertid ascending vertical surface; a, b dorsal; c, d lateral. Crus and foot are not extended far forwards and hind digits flex mesially at end of power stroke, the body is kept very close to the surface being climbed.

Many lacertids climb on open continuous surfaces such as rocks and tree boles and branches. These vary in steepness, from gentle slopes to vertical and even overhanging surfaces, and lizards may run directly up them, or descend, or travel laterally or obliquely. Locomotion in specialised lacertid climbers often has many similarities to that of ground dwellers, but there are marked differences, especially when ascending perpendicular and near-vertical faces.

In this situation, a lizard like *Lacerta oxycephala* climbs with its body very close to the surface and the limbs spread laterally so the distal extremity of the femur does not pass dorsal to the crus during the power stroke (Fig. 14). As in ground dwellers, the limbs work in diagonal pairs. Each hind foot is placed lateral and posterior to the ipsilateral forefoot and the hind leg in each diagonal limb pair is delayed relative to the foreleg so that, as the recovery phase is brief, the proportion of time when two feet are out of contact with the substratum is small. In observed sequences of climbing in *Lacerta oxycephala*, the recovery phase took between an eighth and a quarter as long as the power phase, the smaller proportion being during slow

climbing. Counts of the number of frames of cine film in which four, three and two feet gripped the rock suggest that four legs may be in contact for over half, and three legs for over three-quarters of the total time; there is consequently no floating phase. This pattern contrasts strongly with fast locomotion in specialised ground dwellers where two legs are usually out of contact with the substratum and sometimes all four. The distance between the consecutive foot holds is more or less equal for both fore and hind limbs, being about half to three-quarters of the snout-vent distance in the locomotory sequences studied.

Movements of the hind limb

The excursion of the hind limbs is relatively restricted and although the femur is directed anterolaterally at the beginning of the power stroke (right hind limb, Fig. 14a,c), the crus is not brought fully forwards at this time and is usually, directed approximately normal to the body axis. The metatarsal segment, which is mesially inflected, is then directed anterolaterally and is placed flat on the substratum.



Fig. 15 Flexing in the hind toes of a climbing *Lacerta oxycephala* at the end of the step. a, oblique lateral view showing flexion in the sagittal plane of the toes. b, dorsal view, showing mesial flexion of toes 1-4.

Often the digits are spread radially with all the claws inserted in minor irregularities in the substratum and the well developed toe 5 contributing positively to the grip of the hind foot. Toes 1–3 are often directed more or less anteriorly, 4 laterally or somewhat posteriorly and 5 posteriorly. Sometimes, instead, toes 3 and 4 may both be directed obliquely backwards, or toes 1–4 are all directed forwards.

As the crus flexes on the femur and the body of the lizard moves forward, it becomes directed posterolaterally, changing its orientation to the foot. This results in the metatarsal segment being directed more laterally and its posterior edge rising; because the claws are firmly inserted, digits 1–4 flex mesially to accommodate this change in orientation of the metatarsal segment (right hind leg, Fig. 14b; Fig. 15). There is also a tendency for the crus to thrust diagonally backwards at this stage which accentuates the bending of the toes. At the same time, the proximal parts of toes 1–4 flex upwards in the vertical plane mainly at the following phalangeal articulations toe 1–0/1, toe 2–1/2, toe 3–2/3, toe 4–2/3 and 3/4.

The femur is then retracted and the crus is extended posteriorly relative to it, thrusting the body of the lizard upwards (right hind leg, Fig. 14b). The metatarsal segment does not rise much as a whole but its hind edge continues to do so and, as this happens, the claw of toe 5 becomes detached, followed by that of toe 4 (if this digit is not directed forwards), and then those of the remaining toes as the foot moves rapidly forwards to gain a new grip further up the rock face. This recovery stroke takes place with the foot close to the substratum.

In contrast to ground locomotion, the femur of specialised climbers seems to be rotated forwards around its long axis for most of the step cycle, allowing the limb to work largely in a plane more or less parallel to that of the substratum.

Movements of the fore limb

After its recovery stroke, the forelimb is extended forwards with the humerus directed roughly anterolaterally, the lower limb forwards and the digits broadly spread (right limb, Fig. 14b,d). As the humerus

retracts and the lower limb flexes on it, the latter rotates in a parasagittal plane, becoming orientated first normal to the substratum and then directed posteroventrally as the limb thrusts backwards (right limb, Fig. 14a, c). After this the digits flex dorsally and the claws are then released from their contact with the rock face, as the next recovery stroke begins.

Other patterns of locomotion in specialised climbing lacertids

On less steep surfaces a climbing lizard like *Lacerta oxycephala* shifts to a locomotory pattern essentially similar to that which specialist climbers use on the ground (p. 85). When running down a very steep slope, upward motion is presumably powered substantially by gravity, but descent is controlled by the lizard taking short steps in which the hindlimbs are turned back with toes 4 and 5 and often 3 directed posteriorly (Fig. 16). At the end of a step, in which the femur is not moved much, the ventral tendons of these digits are relaxed, loosening the grip of the claws. The foot is then brought forwards, still directed posteriorly, and the claws flexed and inserted again; after this the leg extends backwards and the cycle is repeated.

Problems of upward vertical locomotion

The problems encountered by a lizard climbing a vertical face are quite different from those of an animal running on relatively level ground. 1. There is a need to keep upward thrust parallel with the surface being climbed. Although the oblique thrust delivered to the

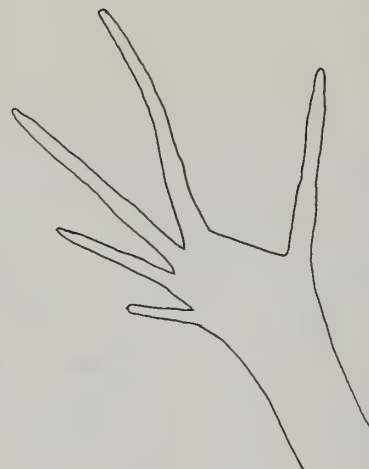


Fig. 16 Position of toes of right hind foot in *Lacerta oxycephala* descending a rock face; 3, 4 and 5 are turned posteriorly.

substratum by the hind limbs of a running lizard tends to push it a way from the ground into a floating phase, gravity returns it rapidly. There is no such automatic restoration of contact on a vertical face and oblique thrust would push the lizard right off the substratum. Thrust must consequently be applied in a direction parallel to the face. 2. There is a constant danger of falling from the face being climbed. In particular, were there no foreleg contact, a lizard would tend to fall outwards because it is then in a position of unstable equilibrium with its centre of gravity above the remaining hindleg contact. The converse condition, with both hind legs free, is less precarious as the posterior part of the body tends to rotate towards the rock. 3. As gravity acts in a direction diametrically opposite to that of locomotion, momentum will be lost very quickly once upward thrust ceases; this must therefore be regular and continuous.

Many characteristics of locomotion, in lacertids that climb vertical faces regularly, appear to ameliorate these problems. Keeping the body and limbs close and parallel to the surface being climbed ensures that backward thrust delivered through the claws is also more or less parallel to it. The danger of falling off the face is minimised by the way the number of feet in contact with it is maximised including those of the particularly important forelegs. This positive engagement of all feet in upward locomotion maximises thrust and makes it available throughout the cycle. Thrust is also maximised by the way flexion of the toes enables the claws to be kept in place as long as possible. Bringing the crus forwards until it is not much more than normal to the body axis is equivalent to moving in a relatively low gear, compared with the anterolateral extension found in ground runners travelling at speed, something that is also appropriate when moving against gravity. Keeping the body and limbs close to the substratum also maximises stride and restricts the downward leverage that the body would exert if it was held away from the substratum. The tail also plays a part in ensuring the foreparts of the lizard do not fall away from the face. It is held very close to the substratum and, if the front legs cannot get a grip (for instance if a piece of smooth card is interposed), the lizard can hold its upright position by stiffening its body and tail and pressing the latter against the surface.

Functional aspects of the limbs and feet of specialised climbing lacertids

The greater equality of fore and hind limb pairs in habitual climbers, when compared with open ground dwellers, is important in allowing the stride lengths of the two pairs to be matched and for the fore feet

to play a positive role in upward locomotion, presumably contributing thrust as well as attaching the foreparts. This contrasts with ground runners where the forelimbs have at most a minor role in delivering thrust. The fact that the hind limbs of habitual climbers are relatively short overall is partly responsible for the low gear nature of upward locomotion, as is the shortness of the crus compared with the femur; when the crus is flexed towards the substratum at some phases of the step cycle, its shortness permits the upper limbs and body to remain close to the substratum.

The short sharp recurved claws on the feet of climbing forms allow a firm grip on substrata like rock that do not permit much penetration. The insertion of the ventral tendon on the distal phalanx of each digit well away from the actual articulation (Fig. 17a, b) means that it has high mechanical advantage and can flex the claw effectively against the weight of the body, ensuring its grip is maintained.

At the end of the recovery stroke, when the hind foot is reattached to the substratum, the long third metatarsal allows the third toe to be deployed easily forwards, laterally or backwards, depending on where its claw can be inserted. The mobility of this toe and of numbers 4 and 5 means that some or all of them can be opposed to the remaining toes to give a positive grip on the substrate. The fact that toe 3 can be turned backwards is also important in allowing its claw to join those of digits 4 and 5 in acting as an intermittent brake when the lizard runs rapidly down steep slopes. When the digits of the hind foot are spread with their claws flexed and in the process of insertion in the rock face, the dorsal and ventral digital tendons contract emphasising the kinking of the phalanges in toes 3–5 and so shortening these digits. This shortening ensures a positive grip by the opposed claws.

Shortness of the hind toes in specialist climbers helps to reduce lateral foot displacement produced by outward thrust of the crus. In the later stages of the power stroke, mesial flexibility of toes 2–4 permits the claws to remain in place. As the metatarsal segment turns more laterally, these toes often become quite sharply bent in a plane parallel to the substratum. This permits the claws to remain in place and upward thrust to be generated for as long as possible. As the back of the metatarsal segment lifts, downward flexion of the second phalanges of toes 3 and especially 4 (Fig. 15a) enable the claws of these often backwardly or outwardly directed digits to remain in place longer, prolonging a positive grip.

Not only do forwardly directed toes flex mesially but, as the metatarsal segment lifts and turns over, hind toes 3 and 4 bend dorsally in the parasagittal plane if they are directed forwards (Fig. 17b). This flexion is concentrated at particular joints which enables it to be more acute than if it were distributed throughout most of the articulations of the toe; the shortness of some intermediate phalanges also contributes to this. Such acute flexion means that the metatarsal segment can stop closer to the rock face instead of being displaced outwards.

Concentration of dorsal flexion is combined with the simultaneous ventral flexion of the claw, necessary to maintain its grip and, in toes 3 and 4 and when backwardly directed, additional ventral flexion of phalanx 2 on phalanx 1. The areas of ventral flexion are produced by tension in the main ventral tendon. Although tension is likely to be more or less the same throughout the length of the tendon, ventriflexion is combined with the intervening area of the toe flexing dorsally. This differential action is an additional result of toe kinking, coupled with the varied positioning of the tendon relative to different articulations in the toe (Fig. 17a, b). Essentially under the joints where the more distal phalanges flex downwards, for instance in toe 4 at the articulation of phalanges 1 and 2 and 4 and 5, the tendon is displaced away from the joint. This differential

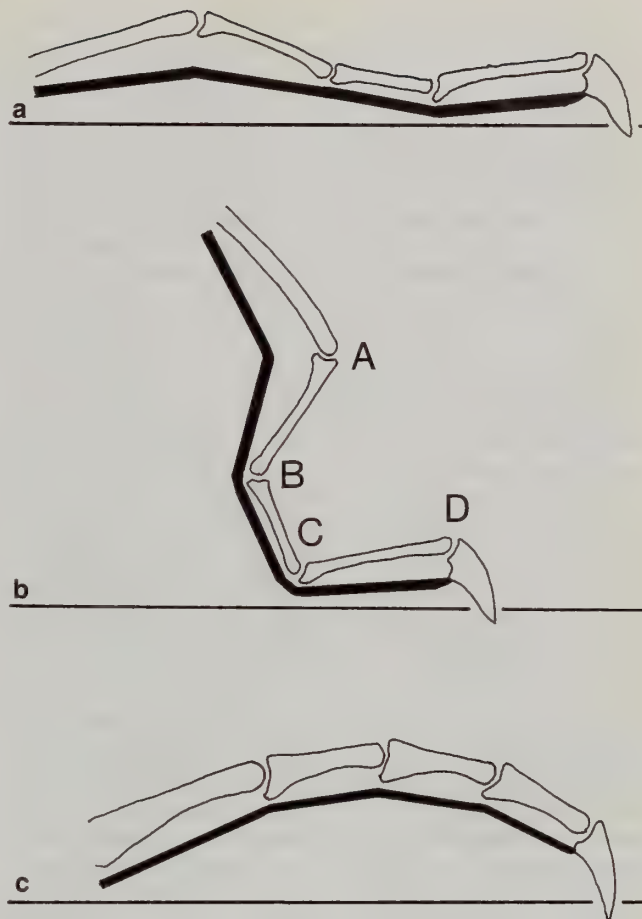


Fig. 17 Effects of digit kinking and tendon position. a. Fourth hind toe of *Lacerta oxycephala* with claw newly inserted in rock face. b. Same toe towards end of stride when metatarsal segment is lifting. Because the ventral tendon (black) is displaced well away from joints A and D and consequently has greater mechanical advantage at them, the articulations can be kept ventriflexed while joints B and C, where the tendon is closer and mechanical advantage less, can simultaneously dorsiflex in response to the movement of the metatarsal segment. Claw grip can consequently be maintained right to the end of the stride. c. Fourth hind toe of *Lacerta agilis*; because there is no inbuilt kinking or marked differential tendon displacement, the toe simply bows upwards when the ventral tendon is under tension

positioning means that the mechanical advantage of the tendon varies with the particular articulation to which it is applying a turning moment; thus advantage is great at the two articulations where it is displaced downwards but weaker in between where, in toe 4, phalanx 2 articulates with phalanx 3 and 3 with 4. Consequently the latter area can flex dorsally in response to lifting and forward movement of the metatarsal segment, while those bordering it retain their ventral flexion, maintaining the lowering of the toe below the level of the metatarsal segment and the grip of the claw. The way the toes of habitual climbers can flex simultaneously in two directions in a plane perpendicular to the substratum and also bend mesially contrasts with the situation in specialised ground dwellers. In these, because joints are double headed and because there is no kinking and the main ventral tendons do not show variation in degree of separation from particular joints, the digits simply curve upwards into a regular arc (Fig. 17c); this places substantial restrictions on the possibility of vertical climbing in these forms (see below).

Kinking of the hind toes of climbing lizards then is a very simple feature that has profound effects on foot function: toes 3–5 can be shortened to provide a positive grip; when directed backwards or outwards, they can be displaced downwards so that they maintain their claw contact with the substratum, even though the posterior part of the metatarsal segment to which they are attached is rising; simultaneous flexing in different directions in the parasagittal plane is possible. Not surprisingly, such a simple but elegant and productive mechanism has arisen many times in climbing lizards (see p. 77). As noted, it seems probable that the numerous variants in the exact pattern of kinking within the foot that are found in lizards as a whole (p. 77) are to a large extent functional alternatives rather than adaptations to different situations.

The forefoot shows some functional similarities to the hind one. The digits are spread very widely when the claws are first inserted and possibly contraction within the palm draws the metacarpals closer, tensioning the fingers. As in the hind limb, the shortness of intermediate phalanges in digits 3 and 4 probably concentrate dorsal flexion allowing it to be sharper and letting the forelimb be turned over without being displaced much outwards. The peculiarities in *Holaspis* have not been investigated in a living animal but they may allow the limb to act even more effectively in a parasagittal plane.

In general the digits of climbing lacertids act differently from those of habitual ground dwellers. Instead of the weight of the animal being balanced on columns of phalanges at times, it is supported by tension in the ventral tendons. The phalanges are subjected to a compressive force by this but, because the tendons are firmly attached by ligamentous sheaths at each joint, such force is along the length of the phalanx and consequently exerts little shear. Also, as the tendon insertion on the claw is offset from the pivot for this on the penultimate phalanx, thus increasing its mechanical advantage, compressive forces along the axes of the toes will be reduced. The largely tensile role of the toes in climbers is reflected in their slender phalanges and robust ventral tendons and the net lateromesial compression of the toe this produces compared with the toes of ground dwellers (Figs. 9b, 10).

Climbing in specialised ground dwelling lacertids

Members of the ground dwelling clade consisting of *Latastia* and its sister group are incompetent climbers. In trials using single lizards of each species, *Meroles reticulatus* could not climb a concrete slab that was at a much steeper than 60° from the horizontal; the maximum angle for *Acanthodactylus erythrurus* and *A. scutellatus* was 70°, and for *A. boskianus* 80°. In these species and other ground dwellers such as *Lacerta agilis*, the hind toes cannot flex mesially or dorsiflect as they do in specialised climbers; as already noted they simply bow upwards instead. In contrast, specialised climbers like *Lacerta oxycephala* and *L. perspicillata* could climb the slab with ease when it was vertical or even overhanging by 10° or 20°.

CONCLUDING REMARKS

Limb proportions and foot morphology of lacertid lizards are obviously evolutionarily plastic and numerous changes in these features have taken place within the family, often in different directions. However, although extreme variants are quite different, virtually no anatomical changes are obviously likely to be irreversible, in the way that loss of phalanges or claws that occur in many gekkotans seem to be. (Development of extra rows of scales on the sides of the toes may be a possible exception).

Across the family, changes in limb proportions and foot structure correlate quite closely with shifts in structural niche and the different

locomotory problems that these entail. It is possible to interpret the different morphologies in functional terms as conferring performance advantage in these situations. Clearly, locomotion in different habitats requires different morphological features, in particular, running on open ground, climbing on open surfaces and traversing vegetation matrixes. Adaptation to any one of these reduces locomotory effectiveness in the others. For instance, the robust, stiff digits that allow ground dwellers to run partly on their toe tips restrict climbing ability, while the flexible toes advantageous to climbers are inappropriate for the most effective kind of ground locomotion. Species which occur in a range of structural habitats consequently must compromise in locomotory terms and are probably not maximally effective in any one situation. Whether they always converge on a functionally intermediate morphology or whether it is sometimes more effective to be efficient in one area but accept penalties in another is not yet clear. However, *Podarcis peloponnesiaca* at Stymphalea, S. Greece, runs effectively on the ground and also climbs readily on rock outcrops but it is very clumsy in the latter situation compared with rock specialists. (Arnold, 1987).

The conflicting mechanical demands of locomotion in different environmental situations and the fact that they are largely unresolvable is one of the main reasons why mechanical aspects of habitat comprise such an important parameter in the structure of lizard communities (Arnold, 1984, 1987). Actually, it is not habitat *per se* that causes the conflict but the fact that really efficient physical compromises seem impossible.

Overall there is great homoplasy among lacertids not only in structural niche but also in the locomotory mechanisms associated with these.

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